Seasonal dynamics of estuarine migration in glass eels *(Anguilla anguilla)*

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Abstract

An analysis of statistical data available in eight glass eel fisheries distributed over the French Atlantic coastline is used to define the upstream migration dynamics of *Anguilla anguilla* in estuaries. The CPUE (Catch Per Unit of Effort) data reveal three different types of seasonal trends that reflect different migration kinetics. The recruitment abundance is studied compared to the salinity of the estuary. The first two types of trends correspond to years of high recruitment and/or of reduced fishing effort. In brackish estuarine zones, the abundances then follow a symmetrical curve, with a peak in January/February. This time course is due to the passage of a wave of migrants. Further upstream, in tidal freshwater zones, the abundances follow an asymmetrical curve which may describe the progressive accumulation of eels between November and March/April. When recruitment is low and/or the fishing effort is high, CPUEs vary during the season following a plateau curve, with values staying more or less constant between November and March. This latter trend represents a balance status between immigration and capture. In this case, abundance indices can only be established with total catches. The curves are explained by the migration behaviour of glass eel which exhibit a resting phase in brackish zones and an accumulation in tidal oligohaline zones. These results have direct consequences particularly for the determination of recruitment abundance indices.

Keywords: Glass eel, *Anguilla anguilla*, catch/effort, fisheries, seasonal trends, abundance, stock assessment.

Dynamique saisonnière de la migration estuarienne des civelles (Anguilla anguilla).

Résumé

Une analyse des séries statistiques de captures par unités d'effort (CPUE), disponibles dans huit pêcheries de civelles réparties sur le littoral atlantique français, permet de caractériser la dynamique de migration anadrome de l'anguille au niveau estuarien. On met en évidence trois types d'évolutions saisonnières qui rendent compte de cinétiques migratoires différentes. L'occurrence de chaque type d'évolution saisonnière varie significativement avec l'abondance du recrutement et la salinité de l'estuaire. Les deux premiers types sont caractéristiques des années de fort recrutement et/ou d'efforts de pêche réduits. Dans les zones estuariennes saumâtres, l'abondance des civelles suit alors une courbe en cloche qui passe par un maximum en janvier-février, traduisant le passage d'une vague de migrants. Plus en amont, dans les zones dulçaquicoles tidales, l'abondance suit une courbe asymétrique qui rend compte de l'accumulation progressive des animaux entre novembre et mars-avril. Lorsque le recrutement est faible et/ou quand l'effort de pêche est élevé, les CPUE varient dans les différentes zones, selon une courbe en plateau, avec des valeurs sensiblement constantes de novembre à mars. Cette dernière évolution traduit un état d'équilibre entre immigration et captures ; l'abondance doit alors être étudiée par l'intermédiaire des captures totales. Ces différents types de courbe sont mis en relation avec le comportement migratoire des civelles, marqué par une phase de stabulation en zone saumâtre et un piégeage naturel des animaux en zone dulçaquicole tidale. Ces résultats ont notamment des implications directes sur la détermination d'indices d'abondance du recrutement.

Mots-clés : Civelle, *Anguilla anguilla*, effort de pêche, pêcherie, variation saisonnière, abondance.

INTRODUCTION

The upriver migration of glass eels (*Anguilla anguilla*) from the sea into freshwaters has given rise to commercial fisheries in several European and North African countries (Eire, Britain, France, Spain, Portugal and Morocco). In France, exploitation developed in the Bay of Biscay estuaries during the years 1960-1970. Because of the economic importance of this fishery (Elie, 1979), scientific surveys were conducted on fisheries in several estuaries. Four sites were studied intensively: the Vilaine, the Loire, the Sèvre Niortaise and the Gironde (*fig.* 1). The surveys of glass eel fisheries distinguished chronological series of catch per unit effort (CPUE) and total catch data (Cantrelle, 1981; Gascuel 1987*a*; Guérault *et al.*, 1986 and 1987).

The CPUE series can be used as indices of the year-to-year variations in glass eel recruitment and therefore provide significant data in a long-term survey of the eel stock variations on a European scale. Moreover, these surveys provided valuable information on the biology of the glass eel and young elver stages. For example, Gascuel (1986) has carried out a study of eel migration behaviour; several authors analysed spatio-temporal variations in abundance and the influence of hydrological or climatic factors on migration (Cantrelle, 1981, Desaunay *et al.*, 1987, Elie and Rigaud, 1984, Gascuel, 1987*a*). Therefore, the analysis of CPUE series has been useful in the study of estuarine upstream migration dynamics of early continental stages of eels and the factors controlling them.

Previous analyses of CPUE data in elver migration have focused on rather short periods and generally on a single site. In every case, CPUEs have been interpreted, at least at the outset, as indices of elver abundance. It has thus been possible to point out the significant fall in the recruitment of glass eels since the beginning of the 1980s, over the whole French Atlantic coast (Gascuel, 1987*b*, Guérault *et al.*, 1987). However, some results show strong geographical or temporal divergences. It is also frequently difficult to distinguish regional trends from local ones.

The first aim is to understand the relationship between CPUE and abundance, so that year-to-year variations in recruitment may be surveyed using fishery statistics. The second is to use the fishery data to interpret biological phenomena, particularly elver migration behaviour and the influence of environmental and seasonal factors.

The seasonal variations in CPUE are compared among zones within estuaries and among estuaries. Year-to-year variations in migration are also examined during a period of declining recruitments which occurred in the 1980s.

METHODS

Glass eel fisheries – Establishment of statistical series

Before the 1960s, glass eel fishing in the estuaries of the French Atlantic coast was a shore-based artisanal fishery employing large dip-nets (0.5-1 m^2 section), with small mesh size (1 mm^2). At the end of the 1960s and the beginning of the 1970s commercial exploitation increased when fishermen began to work from boats, towing one dip-net on each side. The larger dimensions of these nets (generally 1.2-1.5 m^2, but 7 m^2 in the Gironde estuary) enabled the fishermen to exploit most of each estuary. Fishing takes place mainly at night but also during daytime (Cantrelle, 1981; Elie, 1979; Gascuel, 1987*a*).

According to the classification by Elie *et al.* (1982), the catches concern V *b* to VI 1 pigmentation stages between November and March and sometimes VI 2 and VI 3 stages in April. Despite the presence of very pigmented fishes, only 0 stages (less than one year in continental waters) are caught by the fisheries under study (Cantrelle, 1981; Elie, 1979; Gascuel, 1987*a*). Such pigmentation stages, called "civelles" by French fishermen and biologists, concern glass-eels and young elvers. Therefore, we did not make any distinction between "glass-eels" and "elvers" in this paper and both words are used indifferently as a translation of "civelles".

Fishery statistics established by administrative services are frequently inaccurate and unreliable because they do not include any measurement of fishing effort. However, several scientific studies (*table* 1) have concentrated on establishing partial statistics through surveys of a sample of professional fishermen, either by direct interrogation of the fishermen themselves or through the agency of wholesalers who handle the catches of several boats. Therefore, these data are reliable, and allow calculation of the CPUE, expressed as weight of catch (in kg) per boat (*i.e.* per fisherman) and per trip. As a first approach, the CPUE data may constitute an index of daily abundance of glass eels in the fishing zones. Sixteen statistical series, taken from either scientific publications or unpublished studies, have been analysed in this way. They concern eight fisheries, situated in five different estuaries (*fig.* 1), surveyed over 2 to 16 years.

In the Sèvre Niortaise estuary, the first data were collected before 1970 and contain various data on the artisanal fishery. In all other cases, data are from vessel-based exploitation. Nine of the series include daily CPUE throughout the whole fishing season. Seven series only allowed calculation of the monthly average of daily CPUE, because they were the only data in a published report (Gascuel, 1987*a*) and because they were taken from fishermen's logbooks, which do not provide the exact dates.

Table 1. – Characteristics of the sixteen data series analysed.

Fishery location	Salinity type	Series number	Sample size (1)	Study period	Data type (2)	Authors
Vilaine		1	100	1977-78	D	Davoust, 1981
	Brackish	2	10	1979-84	M	Guérault, 1986
	water	3	100	1985-86	D	Guérault, pers. comm.
		4	80	1977-78	D	Davoust, 1981
Loire Downstream	Brackish	5	10	1977-84	M	Guérault and *al.*, 1986
	water	6	80	1984-88	D	Guérault, pers. comm.
Loire Upstream	Freshwater	7	30	1984-88	D	Guérault, pers. comm.
Lay	Brackish	8	6-16	1982-83	D	Gascuel, 1987*a*
	water	9	15-25	1985-87	M	Present study
		10	3	1966-81	M	Gascuel, 1987*a*
Sèvre Niortaise	Freshwater	11	10-11	1982-83	D	Gascuel, 1987*a*
		12	20-25	1985-87	M	Present study
Gironde Downstream	Brackish water	13	1	1979-81	D	Cantrelle, 1981
Gironde-Dordogne	Freshwater	14	20	1980-81	D	Cantrelle, 1981
		15	2-13	1975-79	M	Cantrelle, 1981
Gironde-Garonne	Freshwater	16	1-10	1974-81	M	Cantrelle, 1981

(1) Number of fishermen.

(2) Daily data (D) or Monthly data (M).

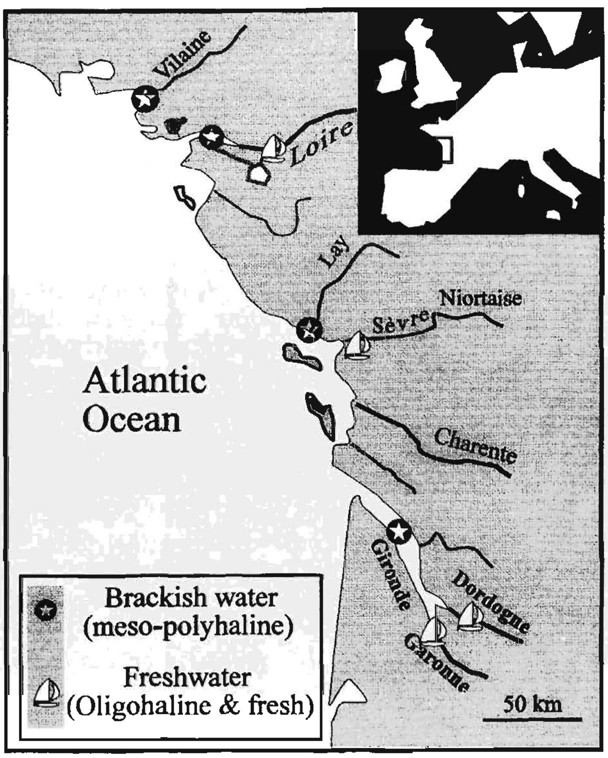

Figure 1. – Location and salinity of the fisheries under study.

Location and ecological characteristics of sites under study

The eight fisheries studied were situated in the estuaries of the Vilaine, the Loire, the Lay, the Sèvre Niortaise and the Gironde. They extend over the tidal reach of these estuaries where the tidal range very between 2 and 6 m. Several basic ecological characteristics essential to glass eel migration vary from site to site.

Salinity

In Sèvre Niortaise estuary, the fisheries are based in oligohaline (<5‰) or fresh waters throughout the whole glass eel migration period. In the Loire estuary and in the Gironde, fishing zones extend over more than 50 km. They comprise meso to polyhaline areas (5 to 30 ‰) situated downstream, next to the river mouths, and oligohaline to fresh waters located upstream, near the tidal reach limit. In the Vilaine estuary, the fishery is located downstream a major estuarian dam and therefore the fishery only extends over a short distance. The salinities are polyhaline most of the time, but they can become meso to oligohaline during the river floods. Such salinities also occur in the Lay estuary. In this study, we only distinguish "freshwater" fisheries (fresh and oligohaline waters), and "brackish" fisheries (meso-polyhaline waters) (*fig.* 1 and *table* 1).

Alternation between flood tidal current and ebb tidal current

In the Sèvre Niortaise and the upstream sections of the Loire and the Gironde (*i.e.* Garonne and Dordogne), variations in water level are principally caused by variations in the speed of the ebb tide current. The penetration of the flood tide current, and consequently the presence of alternating upstream and downstream currents, is dependent on tidal coefficients and the height of floodwater. Within the Sèvre Niortaise estuary, Gascuel (1986) has shown that at each tide, fishing is carried out at the upstream limit of the zone in which the flood tide current is perceptible.

Presence of dams in the estuaries

In the Vilaine estuary, the fishery is situated at river km 9 and it occurs in the region immediately downstream from the Arzal dam which stops the elver's upstream migration. The Lay and Sèvre estuaries are also blocked by estuarian dams but fishing takes place over large downstream zones.

Treatment of data

The series of monthly averages of CPUE were used directly to produce seasonal curves, for each commercial fishery zone and for each year. In order to eliminate erratic fluctuations and short-term variations from the CPUE series, moving averages were calculated for 31 day periods. Each x_i value, representing the CPUE for a given day i, is thus replaced by:

$$X_i = \sum_{d=i-15}^{d=i+15} x_i/31$$

(d: day, x_i: CPUE of the day i; X_i: moving average)

The calculation of standard errors (SE) of each annual average CPUE, expressed in %, attempts to provide an objective criterion to assess the relative importance of variations observed during each fishing season. They are calculated for the middle part of seasons with the daily values (moving averages) or with monthly averages, recorded between December and March inclusive. Before and after these dates, fishing is not carried out at every site and catches are generally low, so the resulting data were not used to calculate the SE.

On the basis of the SE and average monthly values of CPUE empirical criteria were defined to identify different types of seasonal patterns in CPUE variations. Two factors were considered: (*i*) the salinity of the fishery zone; (*ii*) the period under study, with periods distinguished between high abundance (before 1980) and low abundance (after 1980) years.

These correlations were analysed using a Spearman rank-order test, and a Fisher test (*table* 5). We tested the heterogeneity of the interannual CPUE means calculated for each type of seasonal CPUE curve (average from December to March) described on the Sèvre estuary using the Kruskal-Wallis method, designed for use with small samples.

RESULTS

Among sites, fishing generally began in October, with the arrival of the first glass eels. However, the CPUE only became important in November or December. The season ended in April, in accordance with fishery regulations, although in some years the official fishing season may be prolonged until May.

Between December and April, the patterns in daily CPUE (*fig.* 2) or monthly data (*fig.* 3 and 4), differ with the site and the year. Different types of curve were distinguished according (*i*) to the range of variations within a given season (relatively constant curves compared to those with a marked peak) and (*ii*) the situation of this peak when it exists within the season. Among the 65 CPUE series studied, this criterion permitted the distinction of 4 types of curve: symmetrical, asymmetrical, plateau and indeterminate, as discussed below and listed in *tables* 2 and 3. Characteristic curves are plotted in *figures* 2, 3 and 4 for the various study sites.

Symmetrical curves

Symmetrical curves correspond to large-scale variations in CPUE series during a given season, with a peak occurring in January or February. The criteria chosen for the identification of these curves are: (*i*) standard error: SE>30%; (*ii*) CPUE increasing from November to January inclusive; (*iii*) CPUE decreasing from February to April inclusive.

This type of curve represented 26% of the CPUE series. They were observed in all the fisheries except on upstream Loire (*tables* 2 and 3). However, they were much more frequent before than after 1980. Such a seasonal trend is thus characteristic of the CPUEs observed in periods of high recruitment, in brackish estuarian zones. It may be due to the passage of a run of glass eels arriving from the open sea and subsequently continuing their migration towards the upstream zone of the estuaries. The abundance of arrivals increases in this way from October to January-February, then decreases during the spring.

Asymmetrical curves

Asymmetrical curves also reflect large variations in CPUE during the season but with a peak in March or April. The criteria for their identification are as follows: (*i*) Standard error: SE>30%; (*ii*) CPUE increasing from November to March.

This type of seasonal CPUE pattern was observed in 15% of the cases throughout the study period but, in

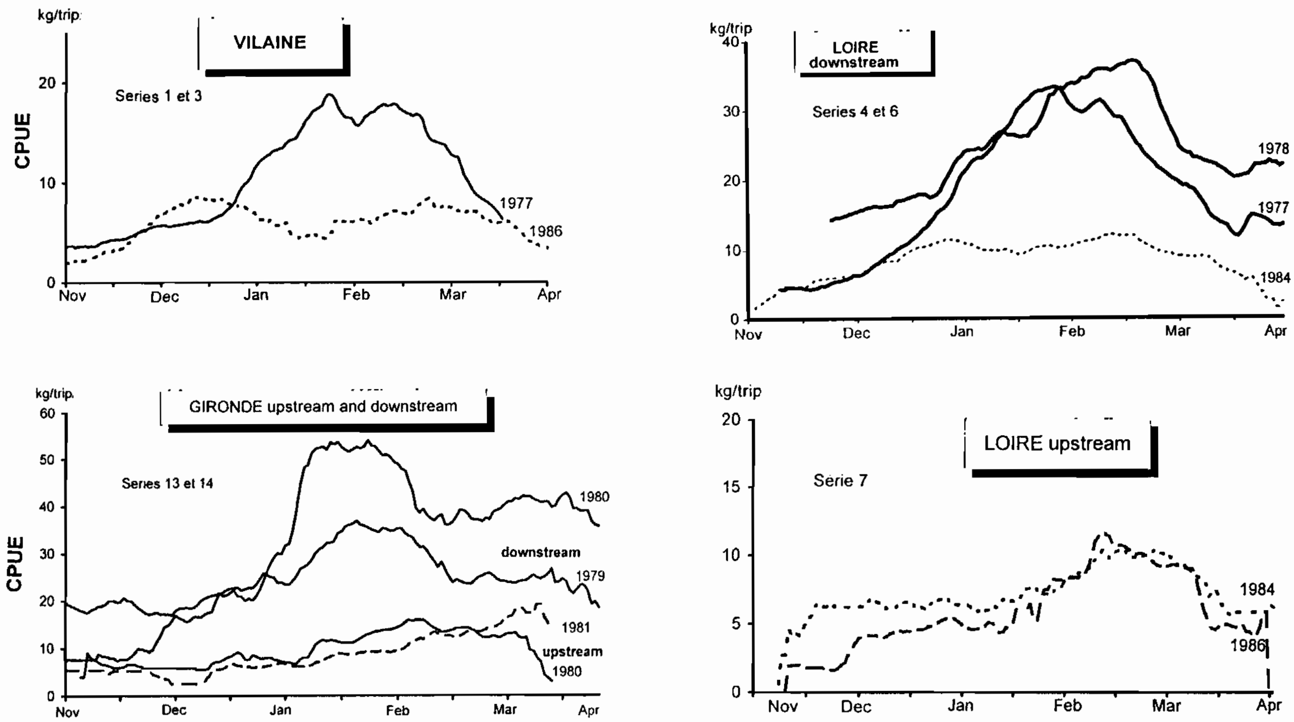

Figure 2. – Seasonal variations in daily CPUE (kg per trip and per boat), showing the three characteristic types of curve (symmetric, asymmetric, plateau) in estuaries of the Vilaine (series 1 and 3), the Loire (series 4, 6 and 7) and the Gironde (series 13 and 14). Series numbers are from table 1. (______ Symmetric curve, – – – Asymmetric curve, ----- Plateau curve).

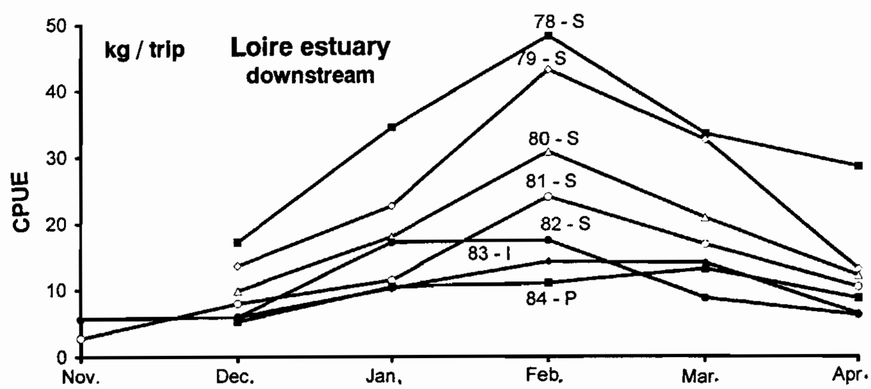

Figure 3. – Seasonal variation of the average monthly CPUE (kg per trip and per boat), showing the three types of curves observed in the downstream Loire estuary between 1978 and 1984 (series 4 and 5, *table* 1).

contrast to the symmetrical curve, it mainly occurred in freshwater fisheries (upper sections of Loire and Gironde estuaries or in Sèvre Niortaise). In this case, it seems that the glass eels, arriving from the open sea, gradually accumulate in the zone during the season and only continue their migration upstream into the riverine system from April onwards.

Plateau curves

Plateau curves were defined by a relatively constant CPUE from December to March. The criterion for their identification is: SE< 20%. This seasonal pattern occurred in 22% of the cases, mainly after 1980 (13 cases against only 1 before 1980), both in brackish and in freshwater zones. It seems to reflect a stable balance between arrivals of glass eels from downstream sectors and population reduction by fishing. Any increase of recuitment is reflected by increased catches. The relatively constant population densities which result may be interpreted as representing the "profitability" threshold of the fishery. Therefore, this kind of seasonal pattern is a result of the influence of the glass eel fisheries on migration dynamics.

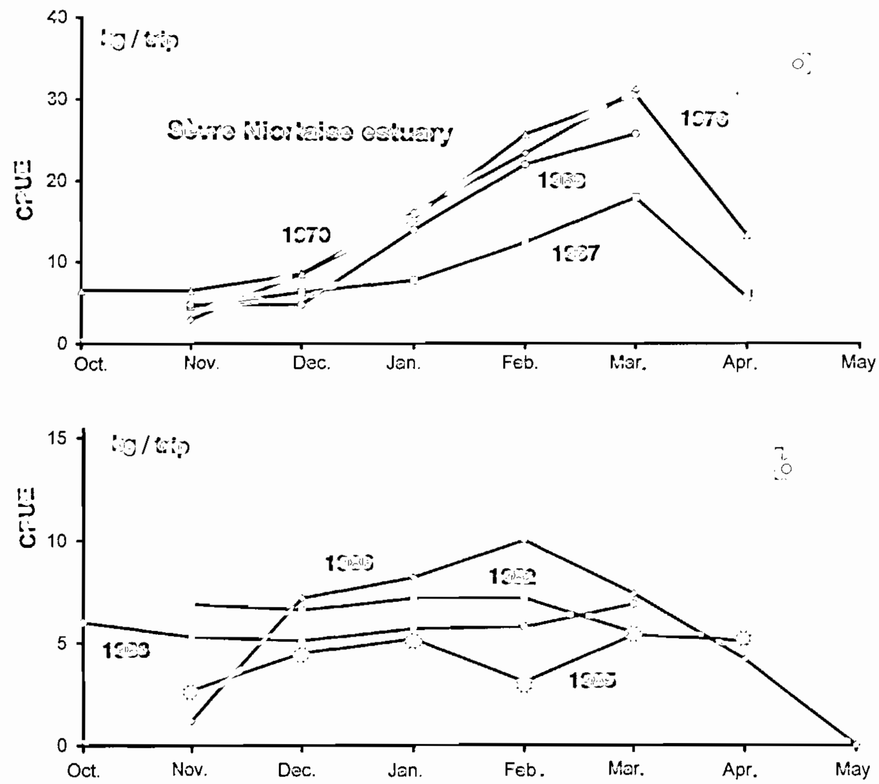

Figure 4. – Seasonal variation of the average monthly CPUE (kg per trip and per boat), showing the two main types of curves observed in the Sèvre Niortaise estuary (series 10 and 12, *table* 1); *a*: Asymmetric curves; *b*: Plateau curves.

Table 2. – Classification of the CPUE seasonal variations, in the eight fisheries (all data series), (S): Symmetrical curve; (A): Asymmetrical curve; (P): plateau curve; (I): indeterminate (see classification criteria in the text).

Year	Vilaine	Loire		Lay	Sèvre	Gironde		
		Upstream	Downstr.			Downstr.	Garonne	Dordogne
1967					A			
1968					A			
1969					S			
1970					A			
1971					I			
1972					I			
1973					I			
1974					S		I	
1975					I		A	I
1976					A		A	S
1977	S		S		S		I	I
1978	I		S		I		I	
1979	S		S		I		I	I
1980	P		S		I	S	S	S
1981	P		S		P	S	A	A
1982	I		S	P	P	I		
1983	A		I	I	P			
1984	P	P	P					
1985	I	I	I	P	P			
1986	P	A	I	P	P			
1987				S	I			

Table 3. – Contingency table: number of curves observed for each type in each environment or years groups.

Year	Salinity Type	Type of seasonal curve			
		Symmetric S	Asymmetric A	Plateau P	Indeterminate I
≤1980	Brackish	8	0	1	1
	Freshwater	6	6	0	14
≥1981	Brackish water	3	1	7	7
	Freshwater	0	3	6	2
All years	Brackish water	11	1	8	8
	Freshwater	6	9	6	16
≤1980	All sites	14	6	1	15
≥1981		3	4	13	9

Indeterminate curves

The fourth type comprises series that do not belong to one of the previous categories. They express generally large-scale fluctuations in CPUE (SE>20%), occurring any time in a given season. These CPUE patterns represent 37% of the observations. This type of curve may be interpreted either as an intermediate stage between the other types, or as the modification of one of them under the influence of major environmental disturbances, such as sudden spates, low temperatures or abnormally low water discharges.

Interpretation of curves - year to year variations

Classification between plateau curves and symmetrical or asymmetrical curves was significantly affected by the fishery period under consideration (*table* 4). In all cases, plateau curves corresponded to average CPUE below 10 kg/fisherman/day (average CPUE December-March).

In the downstream sector of the Loire estuary CPUE fell continuously with a gradual range from symmetrical curves, observed during the years 1978-82, to an indeterminate curve in 1983, and finally a plateau curve in 1984 (*fig.* 3).

In the Sèvre Niortaise estuary high abundance periods are most often represented by asymmetrical curves, but during 1981-1986, plateau curves with low CPUE are mainly observed (*fig.* 5). Here again, indeterminate curves are to be found in an intermediate position, corresponding to medium CPUE.

Symmetrical CPUE series are significantly more frequent in brackish waters than in freshwaters (*tables* 2, 3 and 4). From this point of view, instances of symmetrical curves observed in a freshwater environment appear anormalous. An analysis of the statistical series for the Sèvre Niortaise (*table* 5) helps to explain the phenomenon: the average CPUE of these curves is lower than that of the asymmetrical curves, and is not in fact significantly different from that of the indeterminate curves. Multiple rank-order testing enables us to distinguish three significantly different groups, in rising order of CPUE: plateau curves< symmetrical or indeterminate< asymmetrical curves. Symmetrical curves observed in freshwater environments could thus express intermediate abundance levels and therefore

Table 4. – Correlation analysis between types of seasonal curves and types of environments or years groups and significance level of independence between factors. Differences are not significant when $p > 0.05$.

Tested correlation		Years	Spearman rank		Fisher's test
Type of curve (1)	Factors (2)		Coeff.	Signif. level (p)	Signif. level (p)
S or A	B or F	≤1980	0.53	0.020	0.024
S or A	B or F	≥1981	0.75	0.066	0.114
S or A	B or F	All	0.53	0.007	0.007
P or (S or A)	a or b		0.62	0.007	0

(1) S: Symmetrical curve, A: Asymmetrical curve, P: Plateau curve.

(2) B: fisheries in brackish water, F: fisheries in freshwater, a: after 1981, b: before 1981.

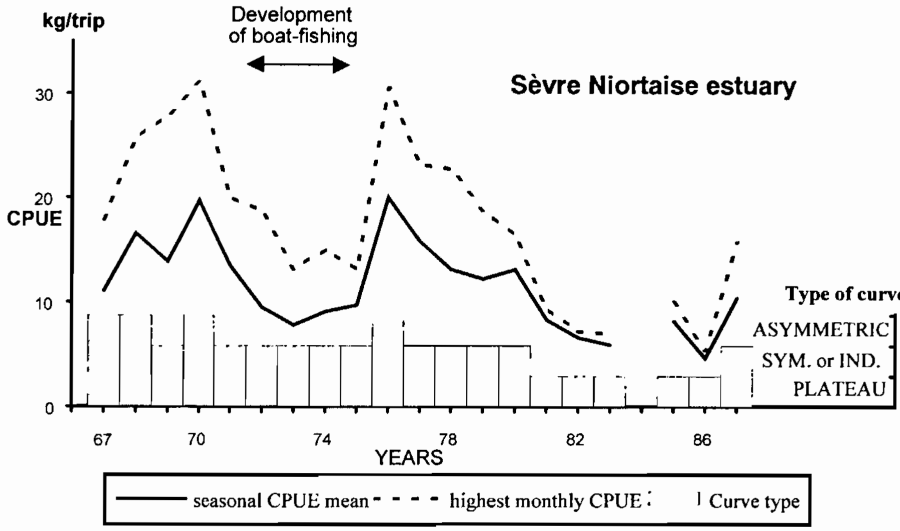

Figure 5. – Evolution of the average annual CPUE (kg per trip and per boat) from November to March and of the maximal monthly CPUE in the Sèvre Niortaise estuary between 1967 and 1986, in relation with the type of curve observed.

Table 5. – Analysis of relationships between types of seasonal curves and CPUE yearly means in the Sèvre Niortaise estuary: average means (from November to March) per type of curve, significance level of hypothesis of CPUE homogeneity between types (Kruskal-Wallis test).

	Types of seasonal curves			
	Asymmetrical A	Symmetrical S	Indeterminate I	Plateau P
Average CPUE (kg/ship/day)	16.8	12.9	11.2	6.3
Asymmetrical	1.00			
Symmetrical	0.16	1.00		
Indeterminate	0.04	0.31	1.00	
Plateau	0	0.01	0.01	1.00

their identification with this pattern of CPUE seasonal series is an artefact probably due to the criteria chosen for classification.

DISCUSSION

Seasonal migration dynamics and migratory behaviour

Estuarine commercial fisheries of glass eels depend upon their migratory behaviour, which is characterised by selective use of tidal currents (Creutzberg, 1958; 1961; McCleave and Kleckner, 1982). During the ebb tide elvers hide in the sediment, and avoid downstream dispersal. During flood tide, they allow the current to carry them upstream but do not swim in any definite direction. The transit of the water masses ensures the migration of the animals. This behaviour, identified by Gascuel (1986), may be described as flow-mediated migration. It results in natural accumulation of glass eels at the upstream limit of the flood tide (Deelder, 1958; Gascuel, 1986).

The freshwater fisheries described in this study are located at this upstream limit (the Garonne, the Dordogne, the Sèvre Niortaise and upstream sector of the Loire estuaries) where the elvers accumulate during the fishing season, a situation expressed by asymmetrical curves. Migration towards the riverine system only begins in spring, with the appearance of active swimming migration behaviour following pigmentation. In these tidal freshwater zones, seasonal migration dynamics, identified by an asymmetrical curve, therefore correspond to two successive behavioural phases, flow carried migration and active swimming migration.

A different type of behaviour occurs further downstream, in the brackish zones in which elvers are carried up and down estuary by the movement of the tides (Deelder, 1958). Hiding during ebb tide is only partial as shown by occasional catches during this time in the downstream areas of the Loire estuary (Elie, 1979) and the Gironde (Cantrelle, 1981). This behaviour contrasts with that observed in tidal freshwater sectors, where ebb tide hiding is total and systematic. Therefore in an estuary like that of the Sèvre Niortaise, elvers are not in the water column during the ebb tide (Gascuel, 1987*a*). It should be noted that this behavioural difference between brackish and freshwater zones also results in different vertical distributions of elvers within the water column during the flood tide (McCleave and Kleckner, 1982; McCleave *et al.*, 1987).

The phase during which the elvers occur in the brackish zone is in fact a temporary period of residency in their upstream migration and results in an increase of their density and therefore of their catchability. Consequently, the distinction between asymmetrical and symmetrical curves is not simply linked to a delay in migration and thus in the abundance peak between the downstream and upstream zones of the estuary. It corresponds to two different types of fishery: one related to the natural stationary phase in the brackish zone, and the other to natural accumulation at the upstream limit of the flood tide current. In the first case the elvers are carried by tidal transport through the fishery zone, in the second they accumulate there progressively. The asymmetrical curve therefore appears as the cumulative function of the symmetrical curve, during the migration season.

Obviously the distinction between the two types of fishery is partly artificial and needs to be modulated according to the sites in question. The Vilaine estuary is an extreme case because the brackish zone and the tidal limit are identical because of the presence of the dam.

Influence of environmental factors

Analysis of environmental factors on glass eel migration dynamics is outside the scope of this study. However, two aspects should be noted. Firstly, the beginning and end of estuarine migration, and therefore the positioning of curves during the year, depends largely on environmental factors. Several authors link the start of migration to the increase of the river flow (Gascuel, 1987*a*; Jellyman and Ryan, 1983). Conversely, the end of the season corresponds to the appearance of active swimming behaviour, which is related to the spring rise in temperature (Gascuel, 1986). This factor also seems to control the beginning of riverine migration (Dahl, 1983; Hvisdten, 1985; Moriarty, 1986) and consequently, the fall in abundance in the estuarine zones.

Secondly, it should be pointed out that the obtained curves correspond to seasonal trends. Short-term fluctuations, depending upon environmental factors, occur within these trends. For example, (*i*) CPUE cyclical variations linked to the alternation of spring tides and neap tides occur (Davoust *et al.*, 1981; Jellyman 1979; Gascuel, 1986); (*ii*) the CPUEs fall when water temperature drops below 6°C because the glass eels remain very close to the bottom (Cantrelle, 1981; Desaunay *et al.*, 1987). These disturbances are strong enough to affect the migration curve itself. In particular, they may explain some of the indeterminate curves.

Determination of annual recruitment and abundance indices

The use of CPUEs as indices of glass eel abundance implies that they are independent from the total fishing effort of the whole estuary. In the case of symmetrical and asymmetrical curves, the proportion of glass eels captured seems low. An increase in fishing effort involves increased catches among the fishery, but the CPUE remain constant. Conversely, an increase of glass eel abundances results in an increase of the CPUE. Therefore, their use as an abundance index appears valid.

On the other hand, when recruitment falls and fishing efforts are intense, seasonal patterns in CPUE follow a plateau curve. Most of the glass eels entering the estuary are caught, and an increase of the fishing

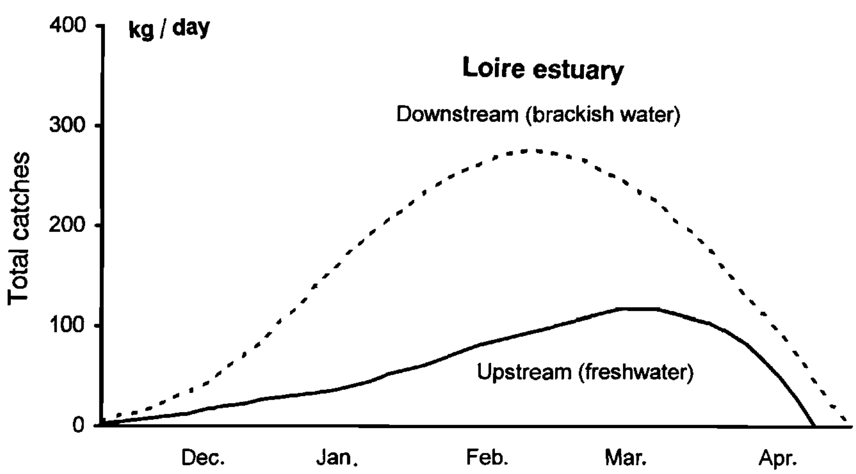

Figure 6. – Fitted functions of seasonal variations of total daily catches observed between 1984 and 1988 in fisheries located upstream and downstream the Loire estuary (Ben Abdallah, pers. comm.).

effort provokes a decline in CPUE. In this case, the recruitment intensity is not directly correlated to the CPUE but to the total catches. In the Loire estuary between 1984 and 1988, the seasonal variations in daily total catches follow symmetrical or asymmetrical curves respectively downstream and upstream in the estuary (*fig.* 6, from Ben Abdallah, 1991), while the CPUEs mainly follow plateau curves (*table* 2, *figs.* 2 and 3).

It must be concluded that the use of average CPUE as indices of annual recruitment in a given site is unreliable where plateau curves are concerned. Its use is only valid if the total fishing effort remains constant within a given fishery over the years. If this is not the case, total captures of the fisheries must be used instead.

CONCLUSION

Successful estuarine commercial fishery of glass eels appears to be related to two types of behaviour: a temporary stay by the animals in the brackish zone, and their natural concentration in the tidal freshwater zone.

In the first case, generally in the downstream area of the estuary, glass eel abundance varies during the year according to a symmetrical curve with a peak in January-February in the estuaries of the French Atlantic coast. In the second case, occurring in upstream estuarine zones, it follows an asymmetrical curve, which represents the progressive accumulation of the animals, from November to March or April. Systematic examination of the CPUEs permits analysis of these seasonal variations but only in periods of high abundance. When recruitment is low, as it has been since the beginning of the 1980s, both upstream and downstream, CPUE seasonal variations generally follow a plateau curve, revealing a state of balance between immigration and captures. In this case, total captures may be used to analyse the abundance variations.

The definition of these different types of seasonal migration dynamics should be useful for further research using glass eel fisheries' data. For instance, the influence of environmental factors on catchability and abundance of glass eels should be analysed in terms of modifications of the CPUE curves or to the underlying total captures seasonal trends. Elsewhere, recruitment indices of glass eels and elvers in estuaries should only be established with CPUE data if the seasonal curves are known. If this is not the case, recruitment indices should be based on total catches.

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REFERENCES

Ben Abdallah L. 1991. L'exploitation des poissons migrateurs dans les estuaires français. Mémoire ISPAR-ENSAR, 138 p.

Cantrelle I. 1981. Étude de la migration et de la pêche des civelles (*Anguilla anguilla* L., 1758) dans l'estuaire de la Gironde. Thèse dr. 3^{e} cycle, Ministère de l'Agriculture, Univ. Paris, Océanogr. Biol., 233 p.

Creutzberg F. 1958. Use of tidal streams by migrating elvers (*Anguilla vulgaris* Turt). *Nature*, 2 p.

Creutzberg F. 1961. On the orientation of migrating elvers (*Anguilla vulgaris* Turt) in a tidal area. *Neth. J. Sea Res.* **1**, 257-338.

Dahl J. 1983. Some observations on the ascent of young eels at the Tange Power dam, river Gudena. FAO/EIFAC Working Party on Eel, Stockholm 1982, 19–22.

Davoust O., P. Elie, G. Fontenelle 1981. Mise au point d'une méthode d'analyse des captures de civelles d'*Anguilla anguilla* L. dans les estuaires de la Loire et de la Vilaine. Cons. Int. Explor. Mer CM 1981/M **34**, 8 p.

Deelder C. L. 1958. On the behaviour of elvers (*Anguilla vulgaris* Turt) Migration from the sea into fresh water. *J. Cons. Perm. Int. Explor. Mer* **24**, 135–146.

Desaunay Y., D. Guérault, P. Beillois 1987. Dynamique de la migration anadrome de la civelle (*Anguilla anguilla*) dans l'estuaire de la Loire : rôle des facteurs climatiques vis-à-vis de la pêche et du recrutement. Cons. Int. Explor. Mer CM 1987/M **18**, 22 p.

Elie P. 1979. Contribution à l'étude des montées de civelles d'*Anguilla anguilla* Linné (poisson téléostéen anguilliforme) dans l'estuaire de la Loire. Pêche, écologie, écophysiologie et élevage. Thèse dr. 3^{e} cycle, Univ. Rennes, 138 p.

Elie P., R. Lecomte-Finiger, I. Cantrelle, N. Charlon, 1982. Définition des limites des différents stades pigmentaires durant la phase civelle d'*Anguilla anguilla* L. *Vie Milieu* **32**, 149-157.

Elie P., C. Rigaud 1984. Étude de la population d'anguilles de l'estuaire et du Bassin versant de la Vilaine : impact du barrage d'Arzal, propositions d'amélioration du franchissement de cet obstacle. Tomes II-III. Publ. Univ. Rennes/CEMAGREF Bordeaux, 172 p.

Gascuel D., 1986. Flow carried and active swimming migration of the glass eel (*Anguilla anguilla* L.) in the tidal freshwater part of a small estuary on the French Atlantic coast (the Sèvre Niortaise). *Helgol. Meeresunters.* 40, 321-326.

Gascuel D. 1987*a*. La civelle d'anguille dans l'estuaire de la Sèvre Niortaise : Biologie, Écologie, Exploitation. Publ. Départ. halieutique, ENSA Rennes **4/1**, 355 p. **4/2**, 204 p.

Gascuel D. 1987*b*. Captures, C.P.U.E., abondances et dynamique de migration des civelles, dans l'estuaire de la Sèvre Niortaise : 1961-1983. FAO/EIFAC Working Party on Eel, Bristol 1986, 12 p.

Guérault D., P. Beillois, Y. Desaunay 1987. L'exploitation de la civelle (*Anguilla anguilla*) en Loire et en Vilaine : indices d'abondance et indicateurs halieutiques. Cons. Int. Explor. Mer CM 1987/M **19**, 22 p.

Guérault D., P. Beillois, Y. Desaunay, D. Dorel 1986. Variations de l'abondance de la civelle au travers des données de production : secteurs Loire et Vilaine. *Vie Milieu* 36, 237-242.

Hvisdten N. A. 1985. Ascent of elvers (*Anguilla anguilla* L.) in the stream imsa, Norway. Institute of Freshwater Research Drottningholm **62**, 71-74.

Jellyman D. J. 1979. Upstream migration of glass eels (*Anguilla* spp.) in the Waikato river. *N. Z. J. Mar. Freshw. Res.* **13**, 13-22.

Jellyman D. J., C. M. Ryan 1983. Seasonal migration of elvers (*Anguilla* spp.) into lake Pounui, New Zealand, 1974-1978. *N. Z. J. Mar. Freshw. Res.* **17**, 1-15.

McCleave J. D., J. J. M. Bedaux, P. G. Doucet, J. C. Jager, J. T. L. Long, W. J. Van Der Steen, B. Voorzanger 1987. Statistical methods for analysis of plankton and nekton distribution, with application to selective tidal stream transport of juvenile American eels (*Anguilla rostrata*). *J. Cons. Int. Explor. Mer* 44, 90-103.

McCleave J. D., R. C. Kleckner 1982. Selective tidal stream transport in the estuarine migration of glass eels of the American eel (*Anguilla rostrata*). *J. Cons. Int. Explor. Mer* 40, 262-271.

Moriarty C. 1986. Riverine migration of young eels *Anguilla anguilla* (L.). *Fish. Res.* 4, 43-58.