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A STUDY OF THE ESTUARIAL MIGRATION OF CIVELLES (*ANGUILLA ANGUILLA* L., 1758) USING INDIVIDUAL-BASED SIMULATION

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ABSTRACT

Quantifying the arrivals of civelles (*Anguilla anguilla*) in continental waters is of considerable importance at the present time, given the apparently diminishing continental stocks. Quantification requires a good knowledge of estuarial migration. Bearing in mind the complexity of the phenomenon and the impossibility of reproducing all the natural conditions of an estuary in the laboratory, the use of a model seems to be a worthwhile method of investigation as a complement to work carried out in the field.

'Individual-based' modelization provides a comprehensive overview of complex phenomena by incorporating the underlying mechanisms that govern the system. Our simulator of the estuarial migration of civelles is based on a combination of spatio-temporal discreteness in the characteristics of the estuarine environment and the migratory behaviour of a migrating individual. The model is mainly adjusted by comparison with the CPUE abundance indices based on the daily declarations of commercial fishermen.

Applying this model has enabled us to advance in our studies of what actually occurs during migration and how temperature affects estuary transit time.

RESUME

La quantification des arrivées de civelles d'anguille (*Anguilla anguilla*) dans les eaux continentales constitue un enjeu actuel important compte tenu de l'apparente diminution du stock continental. Il s'avère que cela nécessite une connaissance fine de la migration estuarienne. Compte tenu de la complexité du phénomène et de l'impossibilité de reproduire en laboratoire l'ensemble des conditions naturelles d'un estuaire, l'approche par modèle semble être une voie d'investigation intéressante et complémentaire des travaux menés sur le terrain.

La modélisation « individus-centrée » permet en s'appuyant sur une importante base de connaissances de comprendre les phénomènes complexes dans leur globalité en intégrant les mécanismes sous-jacents gouvernant le système. Notre simulateur de migration de civelles en estuaire repose sur le couplage entre une discrétisation spatio-temporelle des caractéristiques du milieu estuarien et le comportement migratoire d'un individu en cours de migration. Le calage du modèle se fait principalement par comparaison avec les indices d'abondance (CPUE) issus des déclarations journalières de pêcheurs professionnels.

L'application de ce modèle nous a permis d'entamer une réflexion sur le déroulement de la migration et de montrer l'influence du mode d'action de la température sur le temps de transit en estuaire.

I - INTRODUCTION

Understanding the estuarial migration f civelles[1] (*Anguilla anguilla*) is of major ecological, economic and scientific importance at the present time, since continental stocks are apparently diminishing, according to estimations based on data released by commercial fisheries (ANONYMOUS, 1984; GASCUEL, 1987; MORIARTY, 1987; BRUSLE, 1990; CASTELNAUD *et al.*, 1994).

Owing to the complexity of the phenomenon – sea-to-river migration coupled with a metamorphosis – and the fact that it is impossible to reproduce natural estuary conditions in the laboratory, the use of a model seems to be a worthwhile method of investigation as a complement to the work carried out in the field (JOLIVET and PAVE, 1993) with a view to drawing up management measures.

Individual-based modelization provides a mechanistic approach to the operation of a system (LE PAGE, 1995) and a better understanding of complex phenomena. This type of model seeks to integrate the underlying mechanisms governing the system in order to be able to describe it in its totality (SCHOENER, 1986). It is therefore complementary to the conventional phenomena-based approach used in the various civelle migration models studied by LAMBERT (1995), which use the principle of modelizing the directly observable data of a system.

An individual-based simulator makes it possible to organize, collate and compare the data collected on a particular subject in the field and in the laboratory. Our understanding of a phenomenon can thus be enhanced by testing hypotheses on the simulator (JOLIVET and PAVE, 1993) and forecasts may be made based on different scenarios.

II - METHODS USED

The individual-based simulator of the estuarial migration of civelles works on the link between the spatio-temporal fluctuations of the characteristics of the estuarine environment and the migratory behaviour of a migrating individual.
The model was created using object-oriented programming. This technique is suitable both for representing processes based on individual behaviour and for representing spatial heterogeneity (SAARENMAA *et al.*, 1988). The current attraction for this type of model lies in the parallelism between the object of the programme and the agent of the model, with the translation of the various behaviours then occurring naturally (LE PAGE, 1995).

A - Components of the simulator

The migration zone

The Gironde estuary, the physical framework for this simulator, is 70 km long and 11 km wide, with an average depth of 6 m (figure 1). Only the right-hand side of the estuary has been modelized, this being the bank along which migration takes place.
It should be noted that tidal influence extends beyond this zone.

[1] civelle groups together glass eel and elver (ELIE et al , 1982)

The estuary zone, an ecotone between the sea and fresh water, is heterogeneous because of:

- its variable morphology (variations of up to one kilometre in the larger estuaries),
- the seasonal fluctuations of the masses of water present (daily time steps),
- variations associated with tidal flow (hour and kilometre scales),
- the incidence of flooding (random variations).

An environment such as this can be simulated by a succession of spatial arrangements of various more homogeneous fragments of habitats, known as 'patches'.

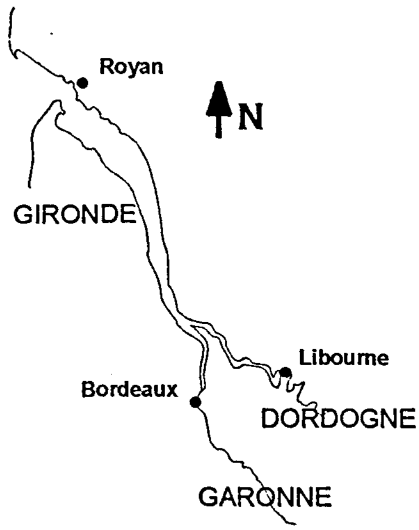

figure 1: Map of the area under study

Civelles and their behaviour

The simulator uses a large knowlegdebase, of which the elements dealing with the anadromous migration of civelles in estuaries have recently been the subject of a paper (ELIE and ROCHARD, 1995).

When migrating in a zone subject to tidal influence, the civelles use the flood tide currents to migrate upstream (FONTAINE and CALLAMAND, 1941) and seek shelter from the ebb tide currents (McCLEAVE and KLECKNER, 1982).

The civelle in its migration phase can therefore be considered as an agent, and more particularly as a reactive agent, since, for example, its movement is halted when the water temperature falls below 4 to 4.5°C (DEELDER, 1952; BEN ABDALLAH, 1991).

B. Operating principle of the simulator

In order to represent the estuarine system we defined one 'ocean' patch, eight 'estuary surface' patches, eight 'estuary floor' patches and one 'river' patch.

The number of estuary patches was selected as a result of the preliminary decision that the length of a patch should equal the average distance covered by a civelle during one tidal cycle (the flood tide lasts a little over 5 hours and the average speed during the flood tide is in the order of 0.5 m/s or 8 km per tide).

Each estuary patch has physical characteristics, temperature and speed of current, updated at each step of the calculation, these factors appearing to be the ones having the greatest influence on civelle migration.

A virtual population of 10 000 civelles was implemented.
Each virtual civelle has constant characteristics during the course of the simulation:

- a date of arrival in the ocean patch, obtained by Gaussian distribution centred on 1 February, since 95% of the individuals arrive between December and March;
- a temperature threshold, obtained by normal distribution, of an average 6° with a standard deviation of 2°;
- an equal mortality rate for each civelle.

The age of a civelle and the estuary patch in which it is situated are updated at each step of the calculation.

Each civelle migrates from patch to patch, from the ocean patch to the river patch, according to methods (elementary actions) that translate our current knowledge of the behaviour of this ecophase.
At each time step, depending on its own characteristics and the characteristics of the patch in which it is situated, a civelle may:

- migrate upwards
- migrate upstream
- migrate downwards
- die.

For example, a civelle may migrate upstream
if it is in a surface patch
if the speed in the patch is strictly positive (flood tide)
and if the stochastic variable (a random number arrived at each time the method is called upon) is lower than the probability of passage defined by the ratio between the speed of the flood tide and the length of the patch.
Temperature only intervenes in the 'migrate upwards' method: a civelle can only use the flood tide current if the water temperature is higher than its own temperature threshold.
All the civelles systematically migrate downwards at the end of each flood tide.
No lateral or downstream movements are currently possible with this simulator.

The first simulation tests were carried out for the 1987-88 season, a year for which we have all the environmental parameters required for the calculations and reliable data regarding civelle fishing in this zone.

This type of model enables us to visualize particular phenomena from different angles: counting individuals and calculating average characteristics (transit time, size, etc.) in the various patches at each time step, monitoring the behaviour of particular animals, the relationship between input and output parameters, etc.

III - RESULTS

The first results obtained were for abundance in each patch and the influence of the temperature threshold on estuary zone transit time.

In figure 2, which shows the course of a civelle's migration through the estuary, the time spent in one patch is represented by a circle of an area proportionate to the amount of time. It can be seen that the time spent in one patch varies according to the location of the patch and the civelle's time of arrival in the ocean patch. For the environmental conditions tested, the average simulated estuary

transit time is 175 hours, which is consistent with the results of marking experiments (CANTRELLE, 1981) and 'migratory wave' monitoring carried out on the same site (ROCHARD, 1992).
It can also be seen that a civelle does not necessarily pass through every floor patch.

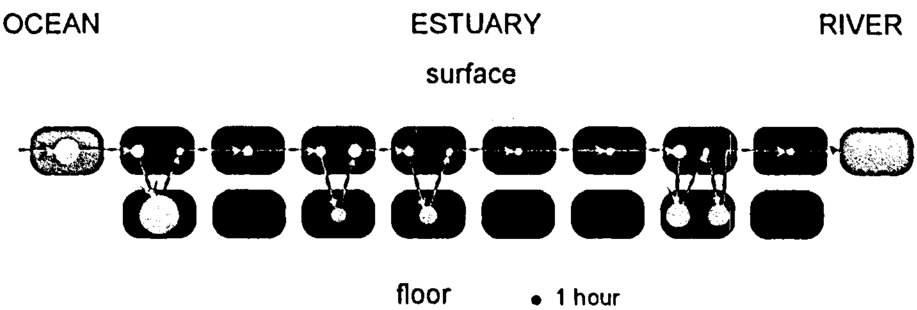

figure 2: Simulated journey of a civelle in the virtual Gironde estuary.
(The area of the circles is proportionate to the time spent by the civelle in the patch)

Abundance curves for each patch (figure 3) were calculated by cumulating all the individual trajectories. It will be seen first of all that the curves are still close to the normal distribution used to define the arrivals in the ocean patch; the deformation induced by the migration methods remains slight. Also, lower densities have been calculated for the upstream patch; this can be explained by the morphology of the estuary which, by narrowing upstream, causes an increase in the speed of the current and therefore means that the civelles stay in the upstream patches for a shorter time. The difference between the peaks for the downstream patch and the upstream patch is consistent with the average transit time.

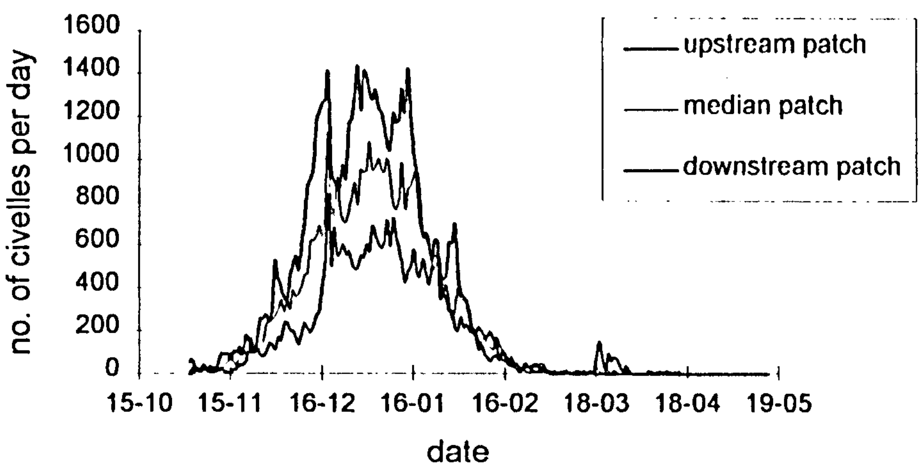

figure 3: Abundance curves obtained in simulation (in number of civelles counted per day in a patch) for three estuary surface patches (1987-88 season).
These curves may be compared to one day's fishing for one boat, supposing that the size of the catch is negligible compared to the stocks present in the patch.
However, the curves cannot be satisfactorily superimposed on those resulting from CPUE data, based on the daily declarations of one or more commercial fishermen in the zone, since curves

produced by the model do not highlight the bimodal nature of the trend observed in the time series of fishing catches (figure 4).

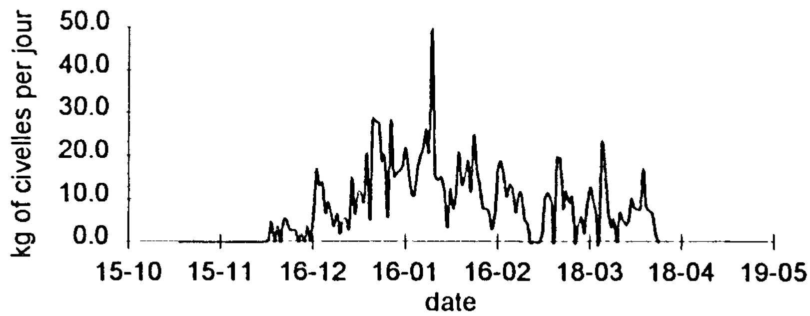

figure 4: CPUE changes through the 1987-88 season

The differences in transit time depending on the civelles' date of arrival in the ocean patch (figure 5) reveals the existence of segregation between civelles with a low temperature threshold, which migrate for around 175 hours, and those with a higher threshold (over 7°C), which are halted by low temperatures and consequently remain longer in the estuary.

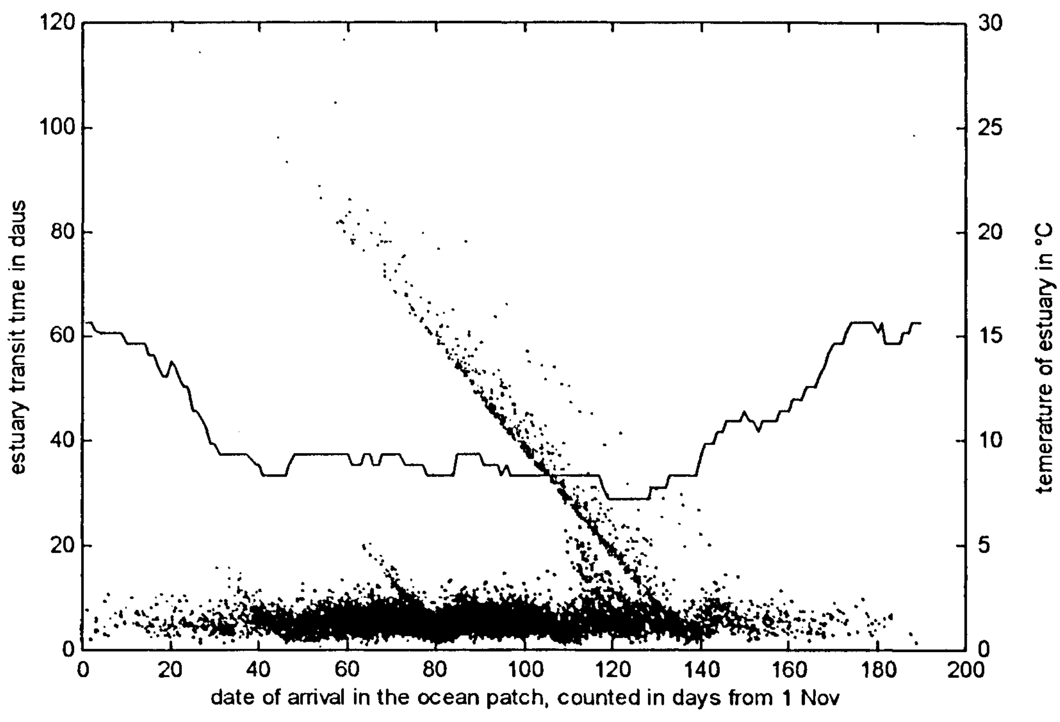

figure 5: Time taken by a civelle to swim up the estuary according to its date of arrival in the ocean patch
(red, civelles with a temperature threshold of over 7°C ; blue lower than 7°C)

IV - DISCUSSION

Very satisfactory at the conceptual level, this type of approach admits the principle that all the individuals differ in their behaviour and physiology, this being the result of a unique combination of genetic and environmental influences (HUSTON *et al.*, in LE PAGE, 1995). This is a relatively accessible and very open-ended type of model. On the other hand, because there is no strict mathematical framework, it is relatively difficult to adjust to actual data. Several avenues could be explored to facilitate adjustment. The first would be to compare the size (or pigmentation stage) structures observed to those produced by the model. Another would be to modelize the fishing strategy, which would then enable us to take account of the bias introduced by commercial fishing. Even if adjustment is difficult, further refinement of the simulator would enhance our knowledge of the estuarial migration of civelles through an "exploration of the possible" (LE PAGE, 1995).
So, although extremely simple, the present version of the simulator enables us to analyse the consequences of the mode of action selected for temperature. The normal distribution of the temperature threshold for each civelle leads to segregation between a group of individuals who migrate rapidly and those which are halted by the cold for varying periods according to their date of arrival. This difference in behaviour gives rise to temperature-dependent estuarial mortality (cold spell), whereas the individual mortality rate is constant. Another question that arises is whether the action of the temperature (or similar action by another exogenous or endogenous parameter) induces sedentarization in the portion of the stock of civelles that migrates slowly.

V - CONCLUSIONS

By collating the information available on the ecology of the migrating civelle, this approach enables us, thanks to simulations using sets of actual environmental data, to test the mode of action of the different environmental factors. By organizing results from different disciplines into a single framework, this type of model facilitates interdisciplinarity and allows us to make fairly rapid advances in our understanding of complex phenomena.

The results of the first operational version of the simulator encourage us to continue our research, particularly by carrying out experiments to verify, confirm or learn more about how migration operates. Physiological studies (changes in the individual thyroxin level distribution of during a tidal cycle and during the season) look promising. Similarly, work on the notion of the age of the civelle (in terms of its stage of pigmentation) must continue to reveal how the behaviour of the civelle evolves over time.
The action of other important factors in migration will soon be incorporated into the simulator, particularly the influence of the diel cycle on the migratory behaviour of civelles (GANDOLFI *et al.*, 1984). Similarly the kinetics of the way civelles swim upstream with the flood tide needs to be looked at in greater detail. These points were the subject of large-scale experiments last winter and the results are currently being interpreted (DEBENAY, 1995).
Finally, a new hydraulic model of the Gironde estuary (JARRIGUE, 1995) should improve estuary speed calculations.

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