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Opinion paper

Assessing the freshwater distribution of yellow eel

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ABSTRACT

Key-words: Anguilla anguilla, *colonization, size classes, logistic model, population management*

In the global context of the decline in wild species, modeling the distribution of populations is a crucial aspect of ecological management. This can be a major challenge, especially for species, such as the European eel, that have complex life cycles, exhibit cryptic behavior, or migrate over long distances. A review of the literature suggests that eel size data could be used to assess and analyze freshwater distribution of eel. We argue that analyses based on small yellow eels (≤ 300 mm) along the longitudinal course of rivers could provide a valuable tool for population monitoring. We propose a standardized catchment recruitment index and a colonization index based on the probability of occurrence (presence/absence data) using logistic models for different size classes. The model developed here provides a convenient guide for assessing yellow eel stages in freshwater areas, and should have concrete applications for management of the species.

RÉSUMÉ

Évaluation de la distribution des anguilles jaunes en eau douce

Mots-clés : Anguilla anguilla, *colonisation, classes de taille, modèle logistique, gestion des populations*

Dans le contexte actuel de déclin des espèces, la modélisation de la distribution des populations est une étape importante pour la gestion de la biodiversité. Cependant, cette modélisation peut s'avérer difficile, particulièrement pour les espèces qui, comme l'anguille européenne, possèdent des cycles de vie complexes, ont un mode de vie cryptique ou effectuent de grandes migrations. Un examen de la littérature suggère que la taille des anguilles peut être utilisée comme critère pour évaluer et analyser la distribution des anguille en eau douce. Nous suggérons que l'examen des patrons de distribution des petites anguilles (≤ 300 mm) le long des réseaux hydrographiques peut fournir des informations précieuses pour le suivi des populations. Nous proposons un indice standardisé de recrutement et de colonisation des bassins versants sur la

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base de l'analyse des probabilités d'occurrence de différentes classes de tailles grâce à des régressions logistiques. Le modèle développé ici fournit un cadre conceptuel et pratique pour l'évaluation des stocks d'anguilles jaunes en eau douce, et devrait trouver des applications concrètes pour la gestion de l'espèce.

INTRODUCTION

Assessing and understanding the distribution of species is a central aspect of conservation ecology. This means that distribution models can be very helpful for conservation planning, and in the general context of biodiversity loss, the literature in this field has grown dramatically in recent years (Guisan and Zimmermann, 2000; Rushton *et al.*, 2004; Guisan and Thuiller, 2005). In this context, one of the main objectives of models is to provide information about the current distribution and trends of a target population. Another objective is to identify the key factors that drive the patterns observed.

However, modeling species distribution poses numerous difficulties. These difficulties arise from constraints that are essentially related to methodology, and they depend to a large extent on the ecological traits of the target species (Rushton *et al.*, 2004); in other words, on the complexity of the life cycle (number of stages and associated habitats), crypticity or rarity. For each context, one has to choose the most appropriate sampling technique and strategy (and the associated scale of investigation) to obtain an appropriate data set. In addition, powerful and reliable analytic methods are needed, and they must be standardized to allow comparisons within and between systems. Finally, even in countries where public opinion is attuned to environmental protection, financial, political and logistical resources for the management of natural spaces are limited (Aronson *et al.*, 2006), and so costs must be kept low. Consequently, devising a methodology for the description and analysis of distribution or abundance patterns can be a real challenge. Besides, species with complex life cycles, extensive habitat requirements and variable density may be very sensitive to anthropogenic factors, and today are often under threat (for example, amphibians and fish in freshwater systems; Darwall and Vié, 2005), and so effective management measures are needed urgently.

The case of the European eel, *Anguilla anguilla,* provides a very good illustration of the problems of distribution modeling. This catadromous, semelparous and long-lived fish (Tesch, 2003) is severely threatened throughout its distribution area (Dekker, 2003a). Larvae (leptocephalii) drift across the Atlantic Ocean in the Gulf Stream to the continental shelf where they metamorphose into glass eels. The tide carries them to the coast, where they transform, first into elvers and then small yellow eels that colonize growth areas. Some of them settle in coastal water and estuaries, but others colonize freshwater (Daverat *et al.*, 2005). This growth stage commonly lasts from 1 to more than 15 years (Rigaud *et al.,* 2008). When they reach a threshold size, they metamorphose into the silver eels that migrate to the Sargasso Sea spawning area where they reproduce just once. Managers need to be able to monitor the freshwater population distribution and assess its current status (Feunteun, 2002; Baisez and Laffaille, 2005). However, such a complex life cycle makes this difficult.

In this study, we present an approach to developing a logistic model for monitoring freshwater eel distribution, which is supported by examples such as those presented in Lasne and Laffaille (2008). We present the conservation and ecological background that led to the assumptions that underlie a standardized catchment recruitment index and a colonization index.

CONSERVATION AND ECOLOGICAL BACKGROUND

> *DEFINING THE PROBLEM AND THE OBJECTIVES*

The European eel has long been considered a stress-tolerant species (Tesch, 2003). However, today it is declining sharply throughout its distribution area (Moriarty and Dekker, 1997; Dekker, 2003b). Although we do not understand the exact causes of this decline, it is speculated that the main factors involved are probably changes in oceanographic conditions that are assumed to be linked to climate changes (Desaunay and Guérault, 1997; Knights, 2003; Bonhommeau *et al.*, 2008), habitat changes and the obstruction of migration by dams and other physical obstacles (Feunteun, 2002; Laffaille *et al.*, 2004, 2007), and the impact of parasites and chemicals (Robinet and Feunteun, 2002; Kirk, 2003). In this context, Russel and Potter (2003) suggested that the precautionary approach is the most appropriate way to consider European eel stock management. Indeed, as we have so little information about the marine phase and are unable to control oceanographic conditions, the best we can do is to optimize the production of spawners (in terms of biomass and quality) in continental areas. In this context, Feunteun (2002) and Baisez and Laffaille (2005) suggest that the best scale of investigation is that of the catchment area. As a first step and for management purposes, we need indicators to monitor the continental stages. Such indicators should make it possible: (1) to assess the current status and trends of the catchment population, (2) to assess the effects of changes in aquatic systems or the efficiency of management measures, and (3) to compare freshwater systems. Such indicators could be combined in a local eel report card. An eel report card seems to be the best way of measuring the impact of the management actions, and providing advice about how to maintain or improve the eel population, taking into account the mortality of the species on the catchment scale (Baisez and Laffaille, 2005).

Yellow eel stock assessments and surveys are common, but they have been based on different sampling methods (Naismith and Knights, 1990; Knights *et al*., 1996; Jellyman and Graynoth, 2005; Laffaille *et al.*, 2005a). They provide evaluations in terms of the relative or absolute abundance, spatial distribution and size- or age-class distribution patterns (Lobon-Cervia *et al*., 1995; Smogor *et al*., 1995; Ibbotson *et al.*, 2002; Laffaille *et al.*, 2004; Laffaille *et al.*, 2005c; Lasne *et al.,* 2008). However, they often only report on a small geographical area. To date, it has not been possible to obtain a description of the state of the whole continental stock (Dekker, 2000). Moreover, local population attributes (*e.g.* mean size, age at maturity, sex ratio, growth rates, body condition, *etc*.) depend closely on the characteristics of the site (Vøllestad, 1992; Panfili and Ximénès, 1994; Dekker, 2000; Yalcin-Ozdilek *et al.*, 2006; Edeline, 2007; Lasne *et al.*, 2008; Lobon-Cervia and Iglesias, 2008; Rigaud *et al.*, 2008), which makes inter-system comparisons very complex. In addition, sampling efficiency depends to a large extent on the kinds of gear, sampling methods and techniques that are used, and these differ from one research team to another (see Naismith and Knights, 1990; Laffaille and Rigaud, 2008; Reid *et al*., 2008). Simple distribution models for the assessment of continental yellow eel population trends on a large scale (*i.e.* at least the catchment scale) are needed to enable us to cope with these problems. Furthermore, large-scale models are particularly convenient for managers (Fleishman *et al.,* 2001), and Collares-Pereira and Cowx (2004) have shown that fish conservation and management actions are most efficient when they encompass the whole catchment area.

> THE "SIZE-DEPENDENT INFORMATION" HYPOTHESIS

Ecological shifts occur throughout the eel's lifetime (Rigaud *et al.,* 2008). As a consequence, the factors that influence eel distribution may also change during the lifetime of individuals. The distribution of individuals at different life stages is bound to depend on and reflect particular processes. Thus, we have to find out what determines the distribution of the various life stages – and in turn, what kind of information assessing them may yield.

Reliability* and *accuracy of information according to size

There may be a high degree of heterogeneity of traits between and within continental populations of eel. In particular, size and age relationships are very variable. Yellow eels range from 0+ to more than 15 years in age, and from just under 70 mm to more than 1300 mm (Rigaud *et al.*, 2008). Differences in individual size may be attributable to age differences as much as to the differences in growth rates that depend mainly on local and/or regional conditions, *e.g.* temperature and salinity of the growth habitat (Yalcin-Ozdilek *et al.*, 2006; Edeline, 2007) and sex (Vøllestad, 1992; Naismith and Knights, 1993; Aprahamian, 2000; Graynoth and Taylor, 2000; Melià *et al.,* 2006). The more time individuals spend in continental waters, the more variable these size-age relationships become (Panfili and Ximénès, 1994; Poole and Reynolds, 1996, 1998; Graynoth and Taylor, 2004). As a consequence, the size of small eels is a better predictor of age than that of large eels, notably silver ones. For instance, we can assume with reasonable confidence that European eels ≤300 mm in length range from 0+ to 4 years (Panfili and Ximénès, 1994; Poole and Reynolds, 1996, 1998; Melià *et al.,* 2006), whereas it is very difficult to age larger eels on the basis of length alone (Mounaix, comm. pers.). In addition, the distribution of large eels results from the combination of all the events the individual has undergone since they reached the freshwater system. As a consequence, it is not possible to extract any precise information from the resulting distribution patterns. Therefore, despite the fact that, as suggested by Feunteun (2002), surveying escaping silver eels is "a major research scope in the coming years" since it is "a relevant way to assess the efficiency of restoration programs because it gives a measurement of the continental dynamics of populations", we think that using seaward migrating dynamics to evaluate the continental population and the efficiency of restoration programs would in fact be neither precise nor parsimonious, because spawner production results from numerous, complex events, some of which may have happened many years earlier. In contrast, far fewer factors influence the distribution of small eels. It would therefore seem to be more accurate and more reliable to base comparisons within or between systems on small eels, because we have more information about them and their recent history. Following this argument, it may be possible to distinguish other classes of smaller individuals, ≤150 mm or 150–300 mm, for instance, and so on, to improve the quality of the data. The smallest eels originate from the most recent recruitment events (0+ and 1+), so focusing on these eels looks like an interesting approach. However, there may be a risk attached to excessively reducing the range of classes, because this would enhance the noise (*e.g.* measurement errors or artifacts), to the detriment of the real trends we want to detect. In addition, the inland penetration of the smallest eels is also limited by the time available to colonize upstream reaches, independently of other factors. Finally, there is a trade-off between accuracy and parsimony in the description of yellow eel distribution. Consequently, we suggest that using two size classes (≤300 and > 300 mm eels) offers a good compromise, particularly as this distinction is biologically relevant.

Differences in the nature of information according to size

Migration behavior, habitat and feeding requirements all change during the continental life of eels (Rigaud *et al.,* 2008). More precisely, several studies suggest that around the 300-mm size several changes occur (Michel and Oberdorff, 1995; Baisez, 2001; Feunteun *et al.*, 2003; Laffaille *et al.,* 2003, 2004). Firstly, elvers and small yellow eels are mainly invertivorous and live in shallow water, whereas larger eels are found in deeper water, where they feed on other fish including small eels. This size-related habitat use on the meso- or microhabitat scale should be taken into account when devising sampling procedures. For instance, the size structure observed could be biased if all the different habitats are not investigated (Laffaille *et al.*, 2003), or if the gear used is not the same (Baisez, 2001). Despite some exceptions (Lamson *et al*., 2006), large eels generally exhibit little migration behavior and tend to become sedentary ("home-range dwellers"), though some remain "nomadic" (Baisez, 2001; Ibbotson *et al.*, 2002; Feunteun *et al.*, 2003; Laffaille *et al.*, 2005b). In UK rivers, Ibbotson *et al.* (2002) showed that density-dependent mechanisms mainly apply to eels aged 0–4 years, whereas larger ones disperse randomly. The environmental and intrinsic factors involved in migration behavior change when individuals grow up, and it is these pressures that determine the distribution of different size classes along the course of freshwater rivers (Feunteun *et al.*, 2003). Thus, the distribution of different size classes on both large and small scales reflects various mechanisms depending on eel size. Finally, 300 mm corresponds to the size from which silvering may occur in males (Dekker *et al.*, 1998; Feunteun *et al.*, 2000; Laffaille *et al.*, 2006). Above this size, individuals may leave freshwater and head for the Sargasso Sea, and so the distribution patterns of > 300 mm eels that we observe may be biased, and the relationships between the factors we are tracking and eel distribution substantially distorted.

PREDICTIONS

This size-dependent information hypothesis enables us to predict continental eel distribution patterns.

> *ASSESSMENT OF FRESHWATER STOCK STATE AND TRENDS*

Several authors suggest that density dependence leads to greater upstream migrations, especially in small eels (*e.g.* Moriarty, 1986; Ibbotson *et al*., 2002; Feunteun *et al.*, 2003; Rigaud *et al*., 2008). In other words, the more the downstream areas are already occupied, the more eels are forced to go upstream to settle in suitable unoccupied places. This has been shown especially in small eels (Briand *et al*., 2005). As a consequence, spatio-temporal surveys of distribution patterns and identification of the "high-density area" (according to Feunteun *et al.*, 2003) of small eels within a catchment area should provide information about downstream occupancy fluctuations. These patterns result mainly from a combination of different parameters: freshwater recruitment (above the tidal limit; see Laffaille *et al.,* 2007), the stock already present (*i.e.* catchment occupancy according to a patchy fluid mosaic as proposed by Feunteun *et al.*, 2003), habitat accessibility (Lasne and Laffaille, 2008) and habitat suitability (Laffaille *et al.*, 2004). Generally speaking, monitoring small eel distribution patterns should provide information about the state of continental stocks. Moreover, since small eels are at the beginning of their continental life, spatio-temporal analysis of small eel distribution should provide indications about future trends in yellow eel stocks and future seaward-migrating silver eel production (Feunteun *et al.*, 2000; Allen *et al.*, 2006). For instance, an expanding upstream distribution (*i.e*. the distance inland colonized) of small eels indicates rejuvenation of the population, whereas a decreasing upstream distribution suggests aging and a future decline in silver eel production.

> *ASSESSMENT OF CHANGES IN RIVER LONGITUDINAL CONNECTIVITY*

Changes in the longitudinal (*i.e.* downstream-upstream) connectivity of rivers are one of the main causes of the decline in eels in local freshwaters (see, for example, Domingos *et al.*, 2006). Feunteun (2002) suggested that the opening of migration pathways was one of the most important management tools, mainly by constructing fishways (Legault, 1994; Knights and White, 1998; Laffaille *et al.,* 2005c) or dam management (Legault, 1990; Laffaille *et al.,* 2007). Scientists and managers need to assess the results of modifications of river network connectivity, and small eels should be good bioindicators of connectivity and permit the detection of dysfunctions (Feunteun *et al.*, 1998; Lasne and Laffaille, 2008). For instance, systems which have no small eels in reaches where they would be expected to be present may suffer from low longitudinal connectivity, and could therefore be targeted for management measures (*e.g*. the installation of ladders, dam removal or dam management). Improvements in the connectivity of river networks can be expected to lead to a rapid recolonization by small eels (see, for example, the case of the River Vilaine, France, in Feunteun *et al.*, 2003 and Briand *et al.*, 2005).

> *INTRA- AND INTER-SYSTEM COMPARISONS OF FRESHWATER SYSTEMS*

It is useful to compare different catchment areas in order to assess global trends (*e.g.* on the scale of the whole European eel population) as well as local ones. Indeed, local abundance and distribution along rivers depend firstly on the number of glass eels that reach the tidal limit, but also secondly on local features, *e.g.* hydrology, size, attractiveness and longitudinal connectivity of the catchment areas, which determine catchment colonization. Similar trends observed across different systems or regions (improvement, reduction or stability of eel distribution) should provide information about the state of the global eel population. On a smaller scale, the comparison of patterns in neighboring catchment areas (which therefore *a priori* have a similar eel input) should provide information about local characteristics, such as longitudinal connectivity or habitat quality (Lasne and Laffaille, 2008).

MODELING EEL DISTRIBUTION IN RIVERS

> *ASSESSING DISTRIBUTION PATTERNS WITH LOGISTIC MODELS*

Various kinds of data can be used to assess eel distribution. Some studies use the absolute or relative density (*e.g.* Lobon-Cervia *et al.*, 1995; Ibbotson *et al.*, 2002; Laffaille *et al.*, 2003; Imbert *et al.*, 2008). The problem with this type of data is that the methods available do not allow reliable standardization of the data due to factors such as differing sampling efficiency in shallow *versus* deep habitats (Naismith and Knights, 1990; Jellyman and Graynoth, 2005). It has also been shown that sampling efficiency is lower at high population densities (Laffaille *et al.*, 2005a). In addition, it is not usually possible to implement any given protocol (*i.e.* using the same sampling gear and the same sampling method) over a large spatial scale. In a recent paper (Lasne and Laffaille, 2008), we showed that logistic models are a very convenient way to assess yellow eel distribution patterns along rivers. Firstly, such models rely on presence-absence data, which are easier to obtain than abundance data (Manel *et al.*, 2001; Royle *et al.*, 2005), especially for eel populations in open and/or large water systems (Naismith and Knights, 1990; Jellyman and Graynoth, 2005). Faced with the widespread problem related to the difficulty of obtaining reliable and usable data sets, recent advances in conservation biology have suggested that presence-absence data are particularly suitable for the assessment of species distribution in a conservation context (MacKenzie, 2005; Vojta, 2005). Despite the simplicity of such input data, they can provide reliable information for analyzing species distribution, especially in a conservation context (Joseph *et al.*, 2006), and above all the distributions of fish assemblages (Ibarra *et al.*, 2005; Lasne *et al.*, 2007a, 2007b), certain fish species (Oberdorff *et al.*, 2001; Pont *et al.*, 2005), migratory fishes (Eikaas and MacIntosh, 2006) and eel (Broad *et al.,* 2001; Lasne and Laffaille, 2008). In fish, electrofishing methods are among the most common ways of sampling fish. Despite its limitations under some conditions (*e.g.* in deep habitats), electrofishing is recognized as being an efficient method of sampling various size classes of eel in freshwaters (Laffaille and Rigaud, 2008). Of course, fish detection is also influenced by the sampling procedure, *e.g.* the surface area prospected, the duration of sampling, number of passes, *etc*. (Laffaille and Rigaud, 2008), but variables of this type could be integrated into the model when sampling protocols across sites are contrasted (Pont *et al.*, 2006, 2007).

Logistic regressions based on presence-absence data can be used to predict the occurrence probability as a function of independent variables (Peeters and Gardeniers, 1998; Broad *et al.*, 2001). Broad *et al.* (2001), who studied eel spatial distribution, constructed the following model:

$$\text{Occurrence probability} = \frac{e^{\beta 0 + \beta 1.X1 + ... + \beta n.Xn}}{1 - e^{\beta 0 + \beta 1.X1 + ... + \beta n.Xn}}$$

where β are regression coefficients, with β0 as the intercept, and X1 to X*n* are the *n* independent variables we want to test, *i.e.* the distance to the tidal limit (km), time (freshwater population trend in a catchment area) and space (comparisons between freshwater catchment areas). The best models are selected according to Burnham and Anderson (2002) using the Akaike Information Criterion (AIC = 2 × log-likelihood + 2*n*, where *n* is the number of estimated parameters).

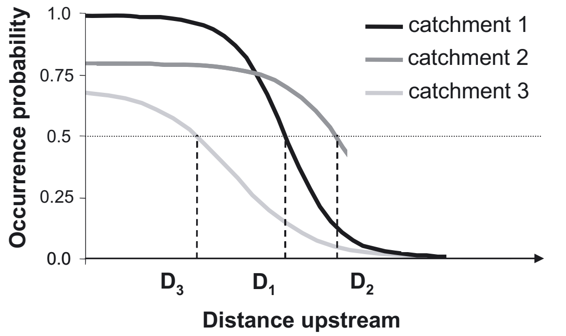

Figure 1
Occurrence probability patterns of small eels (≤300 mm) along three virtual catchment areas. Several metrics can be used to depict catchment patterns, and make inter- or intrasystem comparisons (see text for details). Note that catchment areas 1 and 3 are of equal length, whereas catchment area 2 is smaller.

Figure 1
Patrons d'occurrence des anguilles ≤ 300 mm le long de trois bassins versants virtuels. Différentes métriques peuvent être utilisées pour décrire l'occupation des bassins versants (détails dans le texte). N.B. : Les bassins versants 1 et 3 sont de longueur semblable alors que le 2 est plus court.

> *ANALYSIS OF LOGISTIC DISTRIBUTION PATTERNS*

The general pattern is for the occurrence probability of eels to decrease upstream (Lasne and Laffaille, 2008; Figure 1). However, different patterns may occur in small systems (Laffaille *et al.*, 2003). Several metrics can be used to depict patterns and make inter- or intrasystem comparisons. First, the distance at which the occurrence probability is 0.5 (or, *e.g.*, 0.2 in catchment areas where population densities are low) could be used as an index of catchment colonization resulting in both freshwater recruitment and longitudinal connectivity of rivers. In the example presented in Figure 1, upstream colonization is highest in catchment area 2, and lowest in catchment area 3. Secondly, the occurrence probability in downstream reaches (OP) can be used as an index of freshwater recruitment. On the basis of this assumption, recruitment is highest in catchment area 1 and lowest in catchment area 3. However, the OP in catchment area 2 is lower than that in catchment area 1, whereas conversely, D2 > D1. In such a situation, it is likely that downstream habitat suitability and/or accessibility is lower in catchment area 2 than in catchment area 1.

Such a metric could also be used to assess temporal trends. In Figure 1, catchment areas 1 and 3 could actually correspond to patterns observed for the same system at two different times. Thus, changes in the shape of the curves, and more specifically in the two metrics, could be used to quantify the changes. In the Loire catchment basin, this model revealed size-related distribution patterns, and also showed the consequences of the individual characteristics of the catchment area (*e.g.* in terms of longitudinal connectivity) for these patterns.

CONCLUSION

Despite the complexity of the life history of the European eel, it is possible to produce simple models that are appropriate for management purposes. Exhaustive – and therefore complex – models, such as those based on eel abundance and which integrate a whole set of factors, are also desirable, but so far, it seems to be unrealistic to attempt to develop them on a very large scale, since neither environmental nor fish abundance data are available everywhere or standardized. One of our objectives here was to stimulate the analysis of presence-absence data, and the pooling of data sets from various European countries. Such "pan-European" work using various data sources has been used successfully to develop a fish-based index (Pont *et al.*, 2006, 2007). A European eel model is clearly needed, and we think that it is now a realistic goal. First attempts on the scale of the French territory are currently in process (unpublished data) and they are very promising.

In addition, it seems to be time to develop and use standardized sampling methods (see Laffaille *et al*., 2005a; Reid *et al*., 2008). To guide researchers in such developments, it must be kept in mind that there is a trade-off between the quality/accuracy of data and their volume. Other things being equal, sampling for absolute density data requires a huge investment (in terms of time and/or manpower) and the sampling area is necessarily limited. Conversely, sampling a lot of sites using a short electrofishing session in favorite eel habitats to collect presence data makes it possible to reallocate sampling efforts to other sampling sites. The former approach is probably more suitable for small-scale studies (for instance, to study small-scale patterns), whereas the latter seems to be more appropriate for larger-scale studies.

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