Spatial organisation of European eel (*Anguilla anguilla* L.) in a small catchment

Laffaille P, Feunteun E, Baisez A, Robinet T, Acou A, Legault A, Lek S. Spatial organisation of European eel (*Anguilla anguilla* L.) in a small catchment.
Ecology of Freshwater Fish 2003: 12: 000–000. © Blackwell Munksgaard, 2003

Abstract – Modelling-governing patterns of European eel (*Anguilla anguilla* L.) distribution of four eel size classes (<150, 150–300, 300–450 and >450 mm) in the Frémur basin (northwest France) was done using artificial neural network (ANN) techniques and ecological profiles. Our results demonstrate the high predictive power of the ANN models. Some macro- and microscale factors, such as distance from the sea, depth and flow velocity, have the most significant influence on the models. Influence of distance from the sea appears to be very different from the spatial organisation usually described in river systems. In fact, the general tendencies of total eel densities according to the distance from the sea showed that densities increase weakly upstream. Another outcome was the variations in habitat preference according to the eel size, even if this species is spread over practically every type of microhabitat. Small eels were mainly found in shallow habitats with strong abundance of aquatic vegetation, whereas large eels tend to be found in intermediate to high depth with small to intermediate abundance of aquatic vegetation. Finally, we hypothesise that European eels change behaviour and microhabitat characteristic preference around a size of 300 mm.

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

European eel (*Anguilla anguilla*, L.) is one of the major components of many estuarine and fluvial aquatic systems. It has an important commercial value throughout Europe (about Euro 180 million·year^{-1}), and its biological cycle is long (3–20 years) and remains insufficiently known to develop reliable sustainable management policies. The European eel dominates fish communities of many inland aquatic systems. For instance, in the 1980s, it still represented more than 50% of the fish biomass in estuarine systems such as reclaimed marshes (Feunteun et al. 1999; Baisez 2001) and in rivers of Western and Southern Europe (Moriarty & Dekker 1997), particularly in their downstream reaches (Chancerel 1994; Lobon-Cervia et al. 1995). However, at least since the 1980s, the European eel continental abundance has declined throughout its distribution range, including all accessible European hydrosystems (Moriarty & Dekker 1997; Lobon-Cervia 1999).

Considering the recent scarcity of this species all over its distribution range, ICES recently recommended that all means should be taken to restore the depleted stocks, at all biological stages (ICES 1998). In this focus, one of the most crucial issues is to define the threshold size of the European stock, below which the species becomes threatened with extinction. In this context, several studies have attempted to estimate the size of the stocks using various methods based on fishery surveys (Ardizzone & Corsi 1985), scientific surveys (Feunteun et al. 1998, 2000; Baisez

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2001), or modelling (Dekker 2000). However, most of these studies do not consider the effect of habitat characteristics and the variations in habitat preference according to the size and age, as suggested by preliminary studies in reclaimed marshes (Baisez 2001). This lack of knowledge about precise relationships between densities, sizes and habitats makes it impossible to model eel–habitat relationships and, consequently, to predict the size of eel stocks in river systems. In fact, the density estimates are very often speculative and inaccurate as they do not take the diversity of habitats into account as coastal areas (lagoons and estuaries), deep waters (lakes, large rivers) and floodplain wetlands.

A second key issue is to improve efficiency to restore depleted stocks within river systems: most attempts are based upon improving natural recruitment (fish ladders over obstructions) or restocking. But, recent investigations suggest that habitat restoration should be considered as an efficient option (Feunteun 2002). Here again, knowledge of eel–habitat relationships, and of their temporal variations along the life history of the species, is required to define a hierarchy of the habitats to be restored to efficiently enhance the stocks.

Species–environment relationship models are widely used in applied ecology (Boyce & McDonald 1999) and are generally based on various hypotheses as to how environmental factors control the distribution of species and communities. Besides its prime importance as a research tool in ecology, predictive geographical modelling recently gained importance as a tool to assess the impact of accelerated (i) land use and other environmental changes on the distribution of organisms (see review of Guisan & Zimmermann 2000), and (ii) use of biological resources. The objectives of our study are to analyse the spatial distribution of European eel in a small coastal catchment, characteristic of Brittany (France) rivers, according to the biotic and abiotic environmental descriptors.

Methods

Study site

The Frémur is a small river of northern Brittany (France), which opens into the Channel next to Saint-Malo (Fig. 1). Its catchment covers about 60 km^2, and the overall length of the river and its tributaries is 45 km, comprising 17 km for the main stream. The slope varies between 0.1 and 2% for an average of 0.6%. Despite its small size, the Frémur contains a wide range of habitats from high-velocity streams of the trout zone to lentic
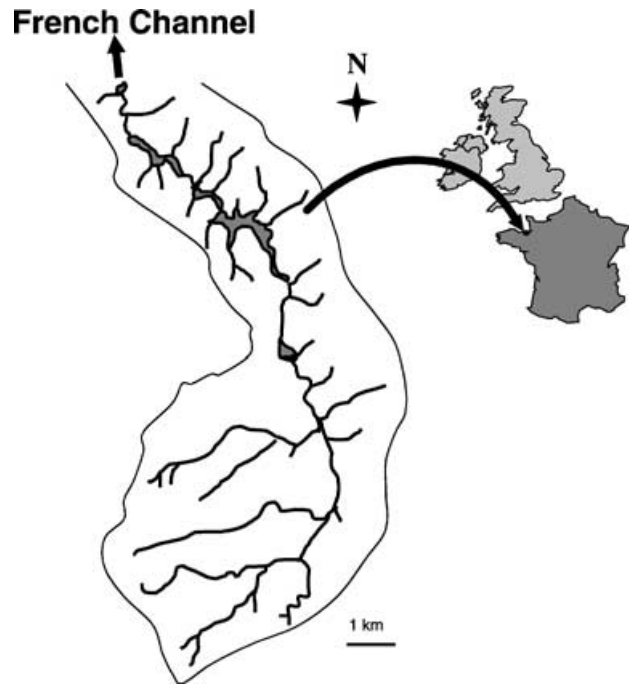

Fig. 1. Study site.

waters of the bream zone in downstream areas, man-made ponds and reservoirs, wetlands, etc. Fishing pressure is quite low on this river (no commercial eel fisheries including glass eels, elvers, yellow eels and/or silvers), and anglers mainly focus on cyprinids, esocids and percids. Therefore, this river appears to be representative of many small coastal catchment of Western France (see Feunteun et al. 1998).

Sampling method

Electrofishing was conducted in 30-m long stream sections delimited by 3-mm mesh stop nets. A 'heron' apparatus was used and delivered direct current (150–365 V and 0.8–6 A). A standardised depletion method (Lambert et al. 1994; Feunteun et al. 1998) was used to assess fish abundance (expressed as number per 100 m^2) using Carle & Strub (1978) estimator (with a minimum of two electrofishing passes). An average of 32 river sections (161 total) were sampled yearly in September from 1995 to 1999. These sectors were located in the mean stream between 1.9 km from the estuary and streams located 16.6 km upstream. Eels were measured (total length, to the nearest millimetre) and released outside the sampled area immediately after their capture. Considering the shallowness of the stream, capturability was very high (on average, $P = 0.70$ in the first electrofishing pass). Therefore, the efficiency of the method appeared to be very good for eel (including large eels)

sampling as it has been stressed in previous studies (i.e., Lambert et al. 1994; Feunteun et al. 1998). The efficiency of the sampling method was tested using fyke nets (5-mm mesh size) and trap and confirmed the scarcity of eels larger than 760 mm long in the catchment (Feunteun et al. 2000).

Several parameters were measured to analyse eel distribution versus habitat conditions. At each sampling section, the distance from the sea (in km) as a macroscale variable was measured from a 1/25,000-scale map. We have measured six microscale habitat parameters that influence spatial organisation of numerous freshwater fish communities, such as water velocity, substratum granulometry, aquatic vegetation, etc. (e.g., Huet 1959; Angermeier & Karr 1983; Oberdorff et al. 2001). These microscale parameters were estimated at each sampling section in order to assess eel microhabitat: two topographical variables, width (in cm) and depth (in cm), one abiotic variable, the flow velocity (in m·s^{-1}), two biotic variables, aquatic vegetation and riparian vegetation expressed as cover index (from minimum 0 to maximum 5) calculated for the whole area of each sampling section, and one substratum composition expressed as modality 1 for silt, 2 for sand, 3 for gravel, 4 for pebbles and 5 for boulders.

The average depth (e.g., average of the maximum depths across a range of stream sections) ranged from 15 to 150 cm. The average widths were 2.5 m (0.5–4.5 m) upstream and 2.9 m (1.5–5.5 m) downstream. Water velocity was measured with electronic flow meter in the bottom (that was essentially used by eels), where flow attains minimum magnitude. Water velocity (e.g., maximal velocity across a stream section) ranged between 0 and 0.3 m·s^{-1} according to the river section. No strong water velocity increment was noted from upstream to downstream reaches, probably because of the shortness of the river (17 km) and its morphology (alternating plains and slopes). Water was fresh (salinities close to zero) in all the sampled stations. Conductivities averaged 410 µS·cm^{-1} and ranged from 300 to 530 µS·cm^{-1}. Vegetation cover consisted mainly of aquatic and riparian vegetation. There was a succession of sections flowing through woodlands, marshes, meadows or cultures (mainly corn) provoking a very heterogeneous vegetation cover. In 65% of the stations sampled, gravel or silt dominated substratum.

Development of the model

Before modelling eel densities according to biotic and abiotic environmental descriptors, a Pearson correlation matrix (with Bonferroni post analysis) was used to show and test significant correlations between variables.

To build models, ecologists use many methods, ranging from numerical, mathematical and statistical methods to techniques originating from artificial intelligence (Ackley et al. 1985), like artificial neural networks (ANN: Colasanti 1991; Edwards & Morse 1995; Lek & Guégan 1999). In this study, we used one of the principles of ANNs, the back-propagation algorithm (Rumelhart et al. 1986). The modelling was carried out in two steps. First, model training was performed using the whole data matrix. This step was used to estimate the ability of the ANN to learn data, especially to calibrate the parameters of models. Secondly, the model was tested using a 'leave-one-out' cross-validation (Efron 1983), where each sample is left out of the model formulation in turn and predicted once. The procedure was repeated for all data to determine the capacity of model for generalisation. This procedure is appropriate when the data set is quite small and/or when each sample is likely to have 'unique information' that is relevant to regression model (Rumelhart et al. 1986; Kohavi 1995), as is frequently found in ecology. This step allows the prediction capabilities of the network to be assessed. The correlation coefficient between observed and predicted eel density was used to quantify the ability of the model to produce the right answer through the training procedure (recognition performance) and the testing procedure (prediction performance).

Five models were developed: one for total eel density and one for the density of each size class (≤150, 151–300, 301–450 and ≥451 mm). These size classes were chosen because they correspond to different phases of the eel's biological cycle, and because these phases have different behaviours and ecology (Baisez 2001). The first size class (≤150 mm) represents elvers recently recruited, which began their colonisation of the river system. The second one (151–300 mm) concerns yellow eels. The two remaining stages (301–450 and ≥451 mm) reflect reproductive status with, respectively, highly sedentary male and female eels. We could have used a single neural network with four dependent variables (one for each of the four size classes), but we preferred to used four networks with the same architecture, each predicting the abundance of one eel size class, so as to easily extract the influence of the independent variables, the environmental conditions.

To determine the relative importance of the parameters, we used the procedure for partitioning the connection weights of the ANN model.

Partial derivatives (PaD) of the network response with respect to each descriptor were used to determine the sensitivity of the environmental variables (Dimopoulos et al. 1999).

Ecological profiles

European eel habitats (spatial repartition of eel densities according to the environmental variables and eel size classes) were visualised in more detail using two methods.

Firstly, we used scatterplots to show fish density according to the macroscale variable (distance from the sea). To obtain maximum ecological reliability, data fitting was performed with a LOWESS (Locally Weighted regression Scatterplot Smoothing) (Cleveland 1979) nonparametric regression model, which is known to reliably fit data tendencies and to respect natural nonlinearity of data (Trexler & Travis 1993). Following Laffaille et al. (2001), we used Lowess smoothing function with $f = 0.80$. The f-value indicates the proportion of samples perfectly fitted by the Lowess smoother; f varies between 0 and 1 according to the sensibility of the analysis and is determined empirically by testing various possibilities and selecting the one, which provides the best generalisation ability to visualise general data tendencies. $f = 0.80$ indicate that 80% of the samples were perfectly smoothed in the smoothing procedure, to provide a high level of accuracy.

[Q1]

Secondly, influence of each microscale variable was visualised independently. Each of the matrices (i.e., for total density and for each size classes) were used to develop ecological profiles, c. preference indices for each environmental variables as a measurement of habitat use by each eel size classes versus habitat availability, based on the method of Ivlev (1961) improved by Beecher et al. (1993) and modified by Brosse et al. (2001). Similar improvements of Ivlev's selectivity index are commonly used for fish habitat use studies (e.g., Coop 1992; Poizat & Pont 1996). Preference was calculated as a normalised ratio of utilisation to availability for different intervals of each environmental variable. Preference indexes were obtained after dividing each variable into several modalities. Their number was defined according to the range of variation of each variable. The following formula was used:

[Q2]

$$I = \frac{\frac{Ob}{Ex}}{\left(\frac{Ob}{Ex}\right)_{\max}} - 0.5$$

where Ob is the density of eels observed for the modality, Ex is the expected density for a theoretical random distribution and $(Ob/Ex)_{\max}$ is the maximum value of (Ob/Ex) for the modality. I varies between -0.5 and $+0.5$. Positive values indicate preference, and negative values indicate avoidance for a given variable. Therefore, values between -0.1 and $+0.1$ can be considered as revealing indifference; from -0.3 to -0.1 and from $+0.1$ to $+0.3$ illustrate slight avoidance or preference, respectively; and from -0.5 to -0.3 and $+0.3$ to $+0.5$ reveal strong avoidance or preference, respectively. To estimate any significant differences between ecological profiles of four different size classes, we used the Wilcoxon nonparametric test (Z).

Results

A total of 4424 European eels were collected. Eel total length ranged from 60 to 880 mm (mean $\pm$ SD $= 236 \pm 117$ mm), and densities ranged between 0.01 and 12.37 eels·m^{-2} (mean $\pm$ SD $= 0.50 \pm 1.08$ eel·m^{-2}).

Among habitat data, the Pearson correlation matrix (with Bonferroni post analysis) showed a highly significant correlation between width and distance from the sea ($r = -0.555$; $P < 0.001$) and between width and depth ($r = 0.580$; $P < 0.001$). To avoid biases, induced by colinearity between variables, width was removed from the data matrix. Consequently, the statistical analyses were performed on six variables. The ANN used was a three-layered (6-3-1) feed-forward network with bias. There were six input neurons to code the six independent variables. The hidden layer had three neurons, determined as the optimal configuration, to give the lowest error in the training and testing sets of data (Lek et al. 1996). The output neuron computes the values of the dependent variables (eel densities).

The scatter plots of eel densities by the ANN models from 500 iterations (best compromise between bias and variance, which is quite low in ANN modelling) showed that the correlation coefficient (r) between observed and predicted values varied from 0.91 to 0.94 for training sets and from 0.78 to 0.86 for testing sets (Table 1). Relationships between residuals and values predicted by the model show nonsignificant correlation coefficients (r Pearson between 0.01 and 0.03 and P between 0.42 and 0.82, both in

Table 1. Correlation coefficient (r) between observed and estimated values in the artificial neural network (ANN) training and testing for the total densities and four size classes of eels.

	Total	<150 mm	150–300 mm	300–450 mm	>450 mm
r training	0.94	0.93	0.94	0.92	0.91
r testing	0.84	0.78	0.84	0.86	0.82

Table 2. Percentage contribution of each independent variable to the prediction of total eel density and densities of four size classes obtained by partial derivatives (PaD).

	Total	<150 mm	150–300 mm	300–450 mm	>450 mm
Distance from the sea	34.7	42.2	33.0	30.2	30.2
Water depth	28.6	25.7	27.5	24.9	24.3
Flow velocity	17.0	16.5	16.5	17.8	21.0
Aquatic vegetation	2.4	0.9	8.2	10.1	5.3
Riparian vegetation	2.0	3.7	0.6	9.9	3.2
Substrate composition	15.3	11.0	14.3	71	16.0

training and in testing set). We can thus consider residuals independent of the predicted values.

The PaD results stress the relative contribution of the independent variables in the ANN models (Table 2). The modelling procedure showed that fish densities were highly connected to two or three major influencing variables: distance from the sea (contributions ranged from 30 to 42%), water depth (from 24 to 29%) and flow velocity (from 16.5 to 21%). Other variables contributed less than 16%.

The general tendency (Lowess smoothing function) is for total eel density to weakly increase upstream (Fig. 2). Moreover, the contribution profile of each eel class density according to the distance from the sea showed different responses (Fig. 3). Small eels (<150 mm) were more abundant downstream than upstream (Fig. 3A). The Lowess smoothing function was more or less linear. Eels between 150 and 300 mm were little influenced by the distance from the sea: the upstream densities were weakly highest in the upstream areas (Fig. 3B). The highest densities of eels >300 mm were located at distances from the sea >10 km (Fig. 3C). This observation was especially evident for large eels >450 mm (Fig. 3D). In summary, this analysis showed a more or less classical downstream–upstream size gradient: small size classes are preferentially located downstream and large size classes upstream. However, total eel densities weakly increase upstream.

Ecological profile of total eel densities (Fig. 4) revealed no significant avoidance and confirmed that there is no microhabitat preference in European eels because of their ubiquitous character, except in this small river for weak flow velocity and the silt.

Wilcoxon's nonparametric test showed non-significant difference between the ecological profiles of the four size classes (Z between 0.284 and 0.943 and P between 0.776 and 0.345). In fact, ecological profile revealed no strong avoidance except for riparian vegetation and only one slight avoidance (Fig. 5). Eels <450 mm avoid strong riparian vegetation cover and eels >450 mm avoid small riparian vegetation cover. The slight avoidance concerned the silt for small eels.

Eels <150 mm and eels between 150 and 300 mm have very similar ecological profile. These small eels preferred shallow habitats (<6 m) with flow velocity >0.1 m·s^{-1}, substrate composed by gravel, pebbles and/or boulders, medium and high aquatic vegetation density, and low riparian vegetation cover. Medium eels (between 300 and 450 mm) have similar preference except that these fish classes do not have preference for depth and substratum composed by sand, gravel, pebbles and boulders. Finally, ecological profile of eels >450 mm differ from that of medium eel in no avoidance of silt and high riparian vegetation cover, in no preference in aquatic vegetation density, and in strong avoidance of small riparian vegetation cover.

In summary, this analysis showed that there is no microhabitat preference in European eels when total density was used, but a shift in localisation of eel size classes according to microhabitat characteristics. Large size classes are located in deeper habitats with less aquatic vegetation density. These size classes are more widespread than small size classes. Small eels are absent or in small density in upstream with high deep and silt. During the eel ascending in the catchment, these habitats were progressively colonised.
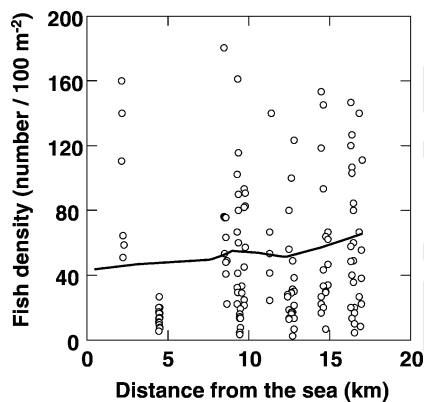

Fig. 2. Scatter-plot of total eel density versus distance from the sea. Smoothing was performed using Lowess nonparametric method (solid lines) with tension (f) = 0.8 (see text for detail).
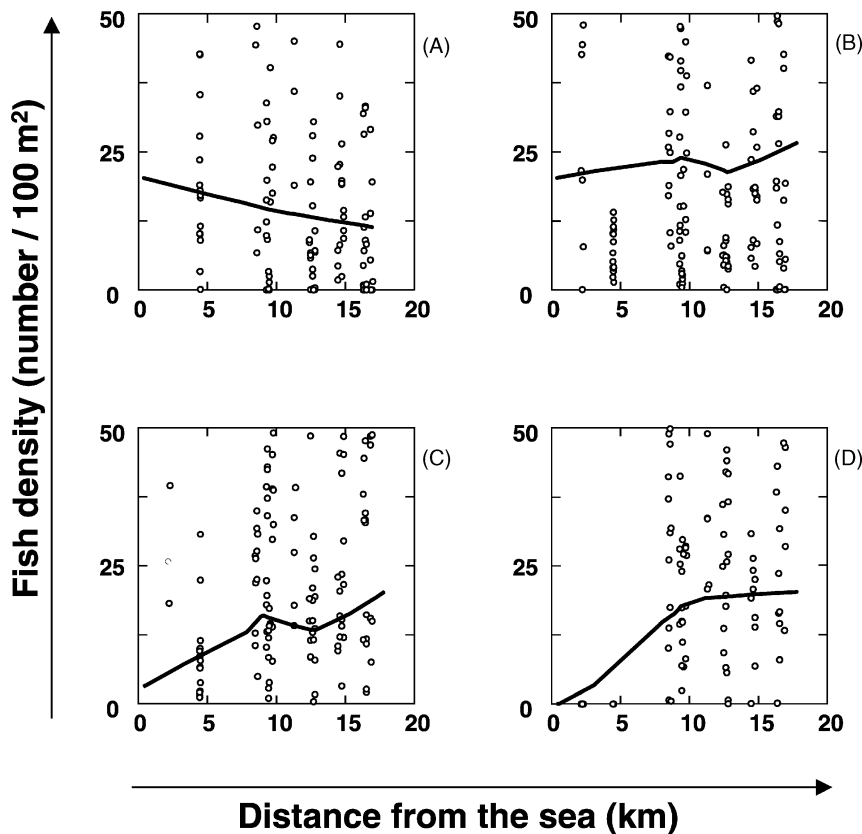
Fig. 3. Location of eel density versus distance from the sea. A: eels <150 mm, B: eels from 150 to 300 mm, C: eels from 300 to 450 mm, D: eels >450 mm.

Fish density (number / 100 m²)

Distance from the sea (km)

Discussion

Since the 1970s, many studies have described the spatial organisation of European eel populations within river systems (e.g., Tesch 1977; Lobon-Cervia et al. 1995; Feunteun et al. 1998; Knights et al. 2001). It is generally admitted that the distance to the sea (macroscale parameter) is the most important structuring parameter for

Fig. 4. Microhabitat profile of total eels calculated for each environmental variable: water depth, flow velocity, substratum composition, aquatic vegetation cover and riparian vegetation cover (see text for detail).

density, average size, age, and sex ratio (e.g., Roche 1988; Naismith & Knights 1993; Lobon-Cervia et al. 1995). In this study, among the environmental variables tested, three had the highest significant effects on the distribution of eels: distance to the sea, water depth and flow velocity. Other variables as substrate characteristics or vegetation cover contribute smallest to the models.

In our study, total eel density tended to weakly increase with increasing distance from the sea. This general pattern appears to be very different from the spatial organisation usually described in many river systems. Only, Oliveira & McCleave (2000) found no density trend for *Anguilla rostrata* in rivers of similar length (but homogeneous river sections) and hypothesised that habitat variables may be a factor. Majority of authors cite eel studies as an evidence of a decreasing density with distance upstream as a general pattern for monospecific eel communities of temperate waters, i.e., for *Anguilla anguilla* (Naismith & Knights 1993; Chancerel 1994; Lobon-Cervia et al. 1995), *A. rostrata* (Smogor et al. 1995; Oliveira 1997), or *A. japonica* (Tzeng et al. 1995). For example, Ibbotson et al. (2002) found that this negative relation accounted for between 19 and 90% of the variation in European eel density in 18 UK rivers.
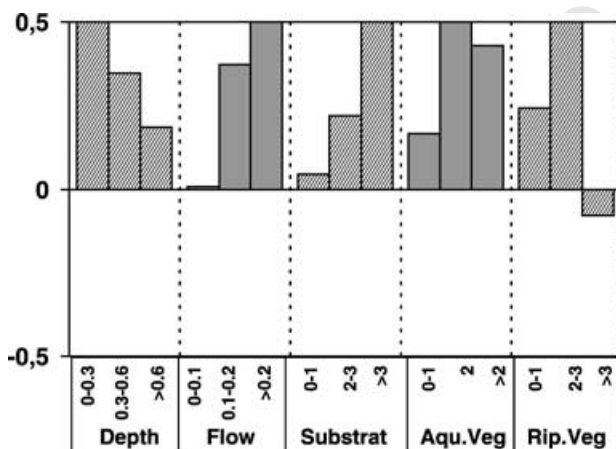
Fig. 5. Microhabitat profile of eels calculated for each environmental variable: water depth, flow velocity, substratum composition, aquatic vegetation cover and ripari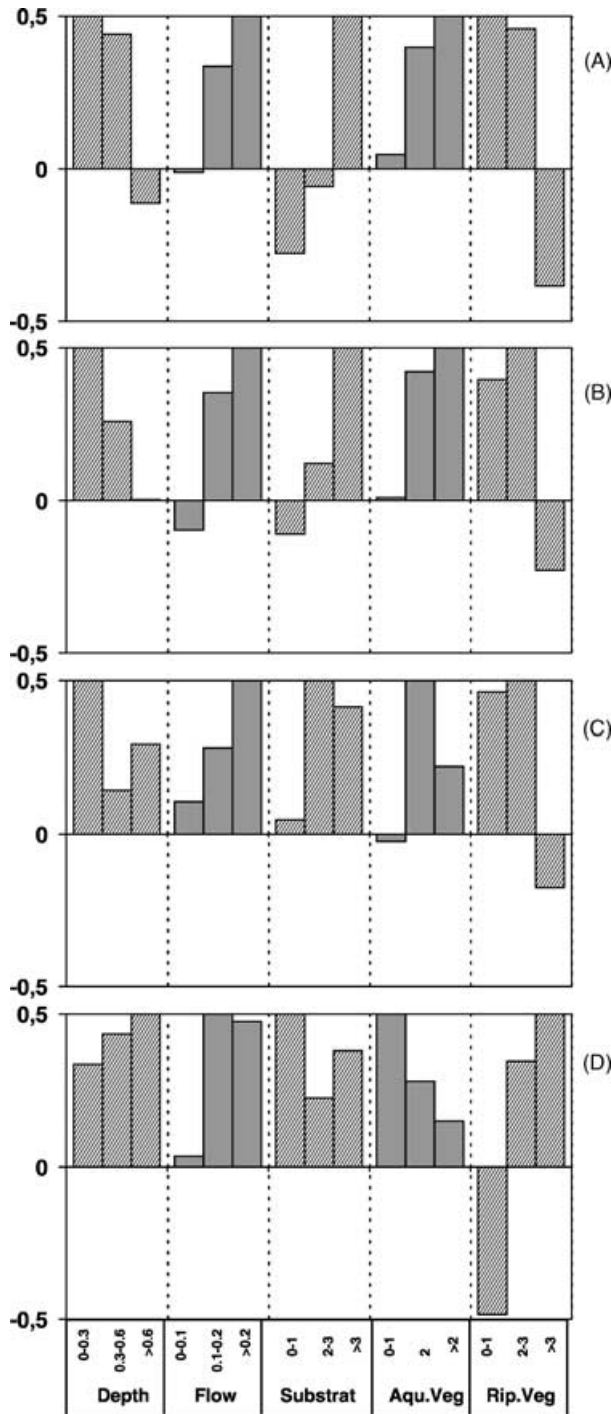an vegetation cover (see text for detail). A: eels <150 mm, B: eels from 150 to 300 mm, C: eels from 300 to 450 mm, D: eels >450 mm.

However, size class analysis provides the evidence that eel size increased with distance from the sea as observed in previous cited studies. Very few age-0 eels (less than 1 year in freshwater) occur despite the short size of the tested rivers (Feunteun et al. 1998), indicating that colonisation occurs

later. The mean size of ascending eels was 133 mm, the majority being elvers (Laffaille et al. 2000). Small eels (<150 mm, dominantly age 1) are mainly concentrated in downstream areas when medium eels (from 150 to 300 mm) weakly tend to increase with upstream localisation. A marked difference occurs for larger eels (>300 mm), which were found at maximum densities in upstream reaches.

It is well known that upstream areas produce a high proportion of females, especially in temperate species (see previous references). However, our observations suggest that the well-accepted hypothesis that faster growth in the lower density areas results in eels developing into females whereas the slower growth in higher density lower reaches results in the production of males (for example, Roncarati et al. 1997) should be re-examined. Invasion mechanisms of river systems are poorly documented (see for example, Ibbotson et al. 2002). One recent theory developed [Q3] (Feunteun et al. 2003) is based upon the identification of four distinct movement behaviours: 'founders' that colonise rivers until they settle in the first available suitable habitat they encounter (future males?) or 'pioneers' that migrate upstream to the upper boundaries of the system (future females?) in the first year; 'home range dwellers', that establish in a given area for several months to several years or 'nomads' that are erratic eels that perform a general upstream shift as they search for suitable areas to forage and/or to settle in the following years.

In our study, classical microscale habitat parameters, which influence spatial organisation of numerous freshwater fish communities such as water velocity, substratum granulometry, aquatic vegetation, etc. (e.g., Huet 1959; Angermeier & Karr 1983; Oberdorff et al. 2001), do not seem to affect eel populations significantly in the ANN models developed. However, even if ecological profiles were very similar whatever size classes, eel distribution showed differences according to depth, substratum composition and vegetation. Small eels are mainly found in shallow habitats with strong abundance of aquatic vegetation, whereas large eels tend to be found in intermediate to high depth with small to intermediate abundance of aquatic vegetation. In summary, eels progressively shift to deeper and unvegetated habitats as they grow.

In river section, Lamouroux et al. (1999) found that eels have significant microhabitat preferences for depth, and that larger eels preferred deeper habitats. The results are consistent with other studies stating that deeper stream sections are primary feeding and resting sites for large tropical

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eels (e.g., Glova 1988; Chisnall & Hicks 1993) and European eel (Baisez 2001). Koehn et al. (1994) showed a positive relation between water depth and fish length. Moreover, the small eels are dominant in areas where vegetation is abundant. Aquatic vegetation is usually assumed to be very important for young fish (Grenouillet et al. 2000), which use this habitat as feeding grounds (Werner et al. 1983; Rozas & Odum 1988). All these conclusions are surely linked with the feeding and moving behaviour of these different sizes. The larger eels, becoming more and more piscivorous with their growth (Michel & Oberdorff 1995), have to explore contexts well adapted with such prey. In contrast, smaller eels have feeding behaviour mainly oriented upon macro-invertebrates whose distribution is significantly correlated with the aquatic vegetation (Clare & Edwards 1983; Scheffer et al. 1984; Painter 1999).

Other variables than catchments and habitats may be a factor that explains spatial organisation. For example, Broad et al. (2002) found that river accessibility to fishers influences size class composition and habitat use by longfin eels *Anguilla dieffenbachi* in New Zealand. Total lengths of from locations inaccessible to eel fishers were normally distributed, whereas those from accessible locations had a non-normal, positively skewed distribution. Mean total lengths and body condition were higher in inaccessible than in accessible sites, consistent with considerable fishing exploitation in the latter. However, fishing pressure was quite low on Frémur river (no commercial eel fisheries including glass eels, elvers, yellow eels and/or silvers). [Q4]

Most studies conclude that there is no microhabitat preference in European eels because of their ubiquitous character, and concluded that no strong habitat index can be developed for European eels (see Knights et al. 2001). For Helfman et al. (1987), American eel (*A. rostrata*) is one of the fish species occupying the widest diversity of habitats. A similar claim can be made for *A. anguilla*, which occurs over similar latitudinal ranges along the eastern Atlantic coastline. This species is spread over practically every type of habitat, and it is quite often the last species that occurs in shallow waters unsuitable for any other species. However, most of these studies do not consider habitat characteristics and the variations of habitat preference according to eel size. River saturation is another factor. Smogor et al. (1995) found that eel distribution differed with density in small coastal catchments: in catchments where eel density was very high, habitat variables were important, whereas in others, distance from the sea governed eel distribution. With densities ranged between 0.01 and 12.37 eels·m^{-2}, the Frémur River was certainly saturated.

From an ecological point of view, the choice of suitable habitats is crucial for individual survival and therefore determines local species distribution (Rosenzweig 1991). Concerning fish, habitat and resource partitioning are regarded as key factors. Moreover, fish distribution permanently seeks a trade-off between available habitat and the necessity to accomplish vital functions (Lévêque 1995). Eel distribution depends upon habitat quality and accessibility, and certainly population parameters as individual behaviour. For example, a number of studies on yellow-phase eels indicate homing and territoriality behaviours. Indeed, *A. anguilla* (Baisez 2001), *A. rostrata* (Helfman et al. 1983; Bozeman et al. 1985; Oliveira 1997), *A. australis* (Beumer 1979; Chisnall & Kalish 1993) and *A. dieffenbachii* (Chisnall & Kalish 1993) have limited movement (a few tens of meters) between daytime resting areas and nocturnal foraging habitats, suggesting the existence of narrow home range. Secondly, telemetry studies have shown that eels displaced from 10- to 100-km return to their initial location (Tesch 1977; Parker & McCleave 1997). Several mark–recapture studies have shown that most eels are recaptured at a few meters from their original capture site. This has been shown in freshwater marshes (Baisez 2001), in river systems of Europe (Feunteun et al., unpublished data) and in estuaries (Secor & Morrison 2001). Thirdly, Lobon-Cervia et al. (1990) have shown that, when density is depleted by fisheries, extremely slow recovery of the population is observed, suggesting that eels from neighbouring areas stay within their home range, regardless of available habitats. When over 300 mm in length, European eel starts to feed regularly on other fish (Michel & Oberdorff 1995) including younger eels in areas with important densities (Baisez et al., unpublished data). This feeding behaviour, associated with territoriality, could be one of the most important causes of the exclusion of small eels in deeper and unvegetated areas. One consequence of this behaviour was segregation between the distribution of eels according to the individual size. Eel habitat preferences change with the individual size. Consequently, we hypothesise that European eels change behaviour and microhabitat characteristic preference around a size of 300 mm. Even if (i) eels progressively shift to deeper habitats as they grow, (ii) and this species is spread over practically every type of habitat, this study (and others, Broad et al. 2001 for example) argues for microhabitat selected by eels. [Q5]

Resumen

1. Modelamos los patrones de distribución de cuatro clases de tamaño (<150, 150–300, 300–450 mm y >450 mm) de anguila (*Anguilla anguilla* L.) en la cuenca del rio Fémur (nor-oeste de Francia). Para ello, utilizando perfiles ecológicos y 'neural networks (ANN)'. Nuestros resultados demostraron un alto poder predictivo por parte de los modelos ANN.

2. Algunos factores a escala macro y micro, tales como la distancia desde el mar, la profundidad y el flujo de la corriente tuvieron una mayor influencia en los modelos. La influencia de la distancia desde el mar parece ser distinta de la organización espacial descrita para sistemas fluviales. De hecho, las tendencias generales de densidades totales de acuerdo a la distancia desde el mar mostraron una tendencia débil de la densidad a incrementar aguas arriba. También lo fueron las variaciones de preferencia de habitat de acuerdo al tamaño de las anguilas

3. Las anguilas pequeñas fueron encontradas fundamental-mente en aguas someras con mucha abundancia de vegeta-ción acuática mientras que las mayores lo fueron en profundidades de intermedias a grandes con pequeñas o intermedias abundancias de vegetación acuática. Final-mente, planteamos como hipótesis que las anguilas cambian de comportamiento y de preferencias de microhabitats a un tamaño de unos 30 cm.

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