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Pascal Laffaille, Aurore Baisez, Christian Rigaud, Eric Feunteun. Habitat preferences of different European eel size classes in a reclaimed marsh: a contribution to species and ecosystem conservation. Wetlands, Springer Verlag, 2004, Vol. 24, pp. 642-651. <10.1672/0277-5212(2004)024[0642:HPODEE]2.0.CO;2>. <hal-00815322>

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To link to this article: DOI: 10.1672/0277-5212(2004)024[0642:HPODEE]2.0.CO;2
URL: http://dx.doi.org/10.1672/0277-5212(2004)024[0642:HPODEE]2.0.CO;2

To cite this version: Laffaille, Pascal and Baisez, Aurore and Rigaud, Christian and Feunteun, Eric *Habitat preferences of different European eel size classes in a reclaimed marsh: a contribution to species and ecosystem conservation.* (2004) Wetlands, Vol. 24 (n° 3). pp. 642-651. ISSN 0277-5212

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HABITAT PREFERENCES OF DIFFERENT EUROPEAN EEL SIZE CLASSES IN A RECLAIMED MARSH: A CONTRIBUTION TO SPECIES AND ECOSYSTEM CONSERVATION

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Abstract: Freshwater reclaimed marshes along the European Atlantic coast are highly suitable for European eels (*Anguilla anguilla*). However, European eel stocks have declined, and the coastal marshes have been subjected to major disturbances. The objective of our study was to analyze the processes governing patterns of European eel microhabitat distribution of four eel size classes (from <160 mm to >360 mm) in a reclaimed marsh (France). Analyses were conducted using artificial neural network (ANN) techniques and ecological profiles. Our ANN results showed that eel densities were significantly related to three major influencing variables: the width of ditch section, the silt depth, and the density of emergent plants. Such ecological profiles were significantly different between small (<240 mm) and large eels (>360 mm): small eels were more widespread than large eels. Large eels were absent or at low densities in shallow ditches with a high aquatic plant cover obstructing the water column and a large quantity of silt. These characteristics seem to define the ditches not directly connected with the main river where dredging operations were rare. Management of regular dredging operations in the channels by maintaining a mosaic of permanent aquatic habitats and avoiding the heavy silt loads in most ditches should be promoted. This dredging operation was probably one of the most promising ways for restoring inland eel stocks.

Key Words: *Anguilla anguilla*, reclaimed marsh, habitat, spatial organization, anthropic disturbances

INTRODUCTION

Salt marshes, estuarine and coastal systems, are among the most productive areas of the biosphere. On the French Atlantic coast, over 230,000 ha of salt marshes have been reclaimed since the 10^{th} century to create land for salt production, agriculture, and aquaculture. These altered systems obviously have new ecological characteristics because they are managed and developed to drain lands, to flood ponds or saltpans, and to control the marine influence (salinity and floods). Therefore, the aquatic habitats form a dense network of more or less interconnected ditches and ponds. The biological carrying capacity of these environments depends essentially on management decisions concerning water and silt levels, salinity, hydraulic connectivity, water residence time, and other environmental factors (Feunteun et al. 1992, Eybert et al. 1998, Feunteun et al. 1999, Baisez et al. 2000).

The habitats of the reclaimed marshes of the French Atlantic coast are highly suitable for an abundant fish community composed of either marine or freshwater species, depending on the salinity, which depends upon management options. Marine straggler species (Clupeidae, Gadidae, etc.) are infrequently found. Marine estuarine-dependant species (Mugilidae, Serranidae, Pleuronectidae, Gobiidae, etc.) are abundant in the marine environment. Freshwater species (Cyprinidae, Gasterosteidae, Exosidae, etc.) are abundant in the freshwater environment. Anadromous (Petromyzontidae, etc.) and catadromous (especially European eel, *Anguilla anguilla* L.) species migrate between the marine and freshwater environment (Eybert et al. 1998, Feunteun et al. 1999, Laffaille et al. 2000a). In both cases, reclaimed marshes provide ideal habitats for European eel, which is the most frequent and abundant species of the fish community. In the 1980s and the early 1990s, eels still represented more than 50% of the fish biomass observed in these areas (Feunteun and Marion 1994, Eybert et al. 1998, Feunteun et al. 1999). Eels occurred in practically every type of accessible habitat, and they were often the only species that colonized the most silty and vegetated ditches or ponds. Biomass ranged from 30 to 300 $kg.ha^{-1}$ depending on habitat characteristics (Feunteun 1994, Feunteun and Marion 1994). Eels therefore represented a valuable resource that was harvested and sold by most farmers, the proceeds accounting for about 10% of their annual income (Feunteun 1994). This income, together with the need to drain pastures, represented one of the major justifications for the upkeep and maintenance of the aquatic network of the marshes by clearing silt and vegetation. These altered wetlands form highly valuable habitats for waterfowl, waders, and species of conservation value such as herons (*Ardea cinerea* L.) (Feunteun and Marion 1994), Montagu's harrier (*Circus pygargus* L.) (Butet and Leroux 2001) and otters (*Lutra lutra* L.) (Beja 1996). The presence of these species in these areas mainly depended upon the management options, which were themselves driven by the exploitation of natural resources, including eels. For these reasons, the European eel can be considered as an umbrella species *sensu* Simberloff (1998), whose restoration and management is profitable for the whole hydrosystem and biocenosis (Feunteun 2002).

However, since the 1950s, these manmade areas have been subjected to major environmental pressures as traditional land use was progressively replaced by intensive agriculture, which involved draining of wetlands, drastically lowering water levels in summer, and use of fertilizers and pesticides. As a consequence, many ditches and ponds were filled in and increasingly interrupted biological connectivity. Consequently, the area of aquatic habitats was reduced about tenfold within 50 years; in the Poitevin marshes, the ditch density was reduced from 150 $m.ha^{-1}$ to 30 $m.ha^{-1}$ and open water areas (relative to close and network water areas) were reduced from 10 to 5% of the total. Similar changes have been reported in a number of coastal reclaimed marshes (Fustec and Lefeuvre 2000). In the same time period, eutrophication provoked algal or cyanobacterial blooms and encroachment by aquatic vegetation (Marion and Brient 1998). Therefore, these highly valuable habitats have been disappearing or have become less suitable for eels.

At least since the 1980s, European eel stocks have declined throughout the distribution range of the species, including all accessible European and North African hydrosystems (Moriarty and Dekker 1997). The same change occurred in the reclaimed marshes (Feunteun et al. 1999, Baisez et al. 2000). In view of the steep decline of the species, ICES (International Council for the Exploration of the Sea) recently considered that ''the species is outside safe biological limits'' (ICES 1998) and that ''all fisheries should be reduced to the lowest possible level'' . . . until a ''global management plan is implemented'' (ICES 1999). This situation is troubling from a socio-economic perspective but also from an ecological perspective because a strong and permanent decline of the local eel abundance could, in some hydrosystems, disturb the balance of the aquatic biocenoses (Feunteun 2002) and even the intersystem fluxes (Laffaille et al. 2000b).

The major causes for the decline are now thought to be habitat destruction and obstruction of migration routes by dams and other chemical or physical obstacles (Feunteun 2002, ICES 2002). The reclaimed marshlands of the Atlantic coast are ideally located to receive glass eel recruits after their oceanic migration. The available habitats are highly suitable for eels.

Therefore, the understanding of the factors governing eel distribution in coastal reclaimed marshes is essential for proposing wetland restoration plans, not only in marine environments, but also along river floodplains or in lakes.

The objective of our study was to quantify the spatial distribution of European eels in a reclaimed marsh ('Marais breton-vendéen', France) relative to both biotic and abiotic characteristics using artificial neural network (ANN) techniques. Predictive modelling has recently gained importance as a tool for assessing the impact of accelerated land use and other environmental changes on the distribution of organisms (see review of Guisan and Zimmermann 2000). Colasanti (1991) found similarities between ANNs and ecosystems and recommended the use of this tool in ecological modelling. Relevant examples are found in very different fields in applied ecology (see review of Lek and Guégan 1999), such as modelling spatial dynamics of fish (Giske et al. 1998, Laffaille et al. 2003). This modelling approach is developed (1) to understand the changes of habitat preference of European eels according to size, (2) to apply these results to the development of a methodology for surveying eel abundance in inland habitats, and (3) to provide a support for the management and the restoration of European eel habitats.

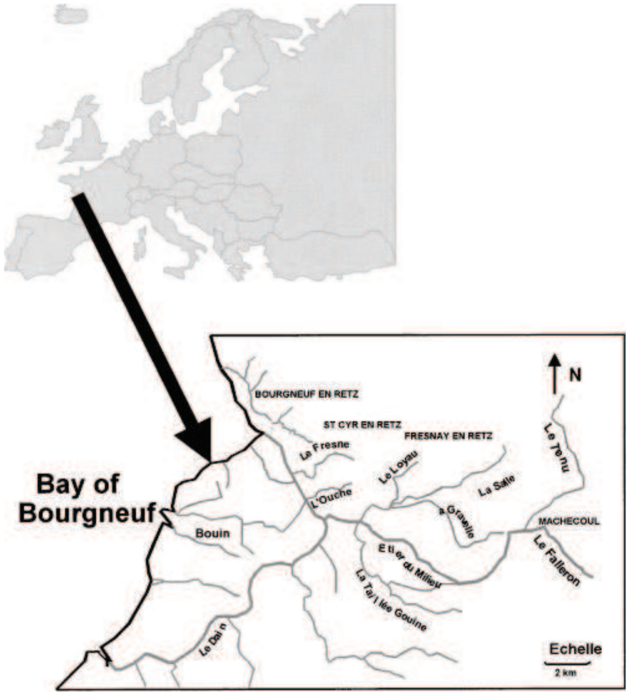

Figure 1. Map of the mash site where habitat eel relationships were studied and its location in the West France (south of Loire River).

MATERIAL AND METHODS

Study Site

The 'Marais breton-vendéen' is situated to the south of the Loire estuary (47° N, 2° W). This flat landscape of 36,000 ha includes 7,200 km of narrow ditches (3- to 4-m mean width, 1.3-m mean depth), with variable characteristics (dredging, silting up, etc.). These ditches are organized in networks with a mean of 200 m.ha^{-1} (Feunteun et al. 1992). They receive water from a natural river catchment, the Falleron, but an artificial water supply from the Loire River is via a pump (Figure 1). The study took place in a 3,000-ha area in the northern portion of the marsh, representative to freshwater marsh (Rigaud et al.1996).

Sampling Method

Electrofishing was conducted in stream sections at least 30-m long delimited by 3-mm-mesh stop nets, in sample areas of about 120 m^2. A 'Heron' apparatus (see Lamarque et al. 1978) was used and delivered a direct current (150 to 365 V and 0.8 to 6 A). A standardized depletion method (Lambert et al. 1994, Feunteun et al. 1998) was used to assess fish abundance (expressed as number 100.m^{-2}) using the Carle and Strub (1978) estimator. Eels were caught in two consecutive electrofishing passes using a modified Point Abundance Sampling by Electrofishing (PASE) technique (Nelva et al. 1979). At each point, the anode was swiftly immersed to the bottom of the ditch and was turned in an area of 1 m^2 around the same spot for at least 30 seconds, and then until all the eels spotted were caught. This was the minimum duration that was effective in provoking a response from the eels present in the vicinity of the anode (see Feunteun 1994). Fish were then collected with fine-mesh dipnets. The mean number of sampling points was 27.3 ± 8 per ditch section. The Carle and Strub (1978) estimator was the method that produced statistically reliable estimates (Cowx 1983). Because of the shallowness of the ditch, capturability and sampling efficiency were high (on average, p = 0.70 in the first electrofishing pass), as observed in previous studies (Lambert et al. 1994, Feunteun et al. 1998, Baisez 2001). The efficiency of the sampling method was quantified using fyke nets and traps and confirmed the scarcity of large eels in the catchment (Baisez et al. 2000, Baisez 2001). Eels were measured (to the nearest mm) and released outside the sampled ditch section immediately after their capture.

An average of 28 ditch sections (not the same every year) were sampled yearly in June from 1996 to 2000, with a total of 141 samplings. Several local environmental variables were measured to analyze eel distribution in relation to microhabitat conditions: (i) three topographical variables: section width (cm), water depth (cm), and silt depth (cm) and (ii) three biotic variables: emergent plants on the ditch bank (mainly composed of *Carex* spp. and *Juncus* spp.), floating-leaved plants (mainly *Lemna* spp. and *Hydrocharis morsus-ranae*), and submerged plant beds in the water column (*Ceratophyllae*, *Potamogeton sp., Myriophyllae*, *Elodea Canadensis* Rich.) expressed as a cover index (from minimum 0 to maximum 5) calculated for the whole area of each sampling section (see Baisez 2001 for more details).

Development of the Model

Fish size-class groups were identified with cluster analyses of the fish densities at each sampling site using Ward's method. This method uses the average value of all objects in one cluster as the reference point for distances to other objects and normalized Euclidean distances (i.e., root mean squared distances).

Prior to ANN modelling, a Pearson correlation matrix (with Bonferroni post analysis) was used to test independence of the variables used in the ANN models. We used one of the principles of ANN, the backpropagation algorithm (Rumelhart et al. 1986). The network was trained using an error backpropagation training algorithm. This algorithm adjusts the connection weights according to the backpropagated error computed between the observed and the estimated results. This is a supervised learning procedure that attempts to minimize the error between the desired and the predicted outputs (see Gevrey et al. 2003 for more details). 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 performance of the ANN for calibrating the parameters of the models and to study the contribution of each independent variable. Second, a jacknife cross validation test (Efron 1983) was performed. Each sample was left out of the model formulation in turn and predicted once. 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 the regression model (Rumelhart et al. 1986, Kohavi 1995). This step was used to assess the prediction capacity of the network. 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).

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). The PAD method was found to be the most useful, as it gave the most complete results (Gevrey et al. 2003).

Ecological Profiles

European eel habitats (spatial distribution of eel densities according to the environmental variables and eel size classes) were examined in more detail using ecological profiles. The influence of each variable was examined independently. Ecological profiles (preference indices for each environmental variable as a measure of habitat use by each eel size class vs. habitat availability) were developed for each size-class matrix, based on methods that have evolved over the last 40 years (Ivlev 1961, Beecher et al. 1993, Brosse et al. 2001). Preference was calculated as a normalized ratio of utilization to availability for different intervals of each environmental variable. Preference indices were obtained after dividing each variable into several classes. Their number was defined according to the range of variation of each variable. The following formula was used:

$$I = [(Ob/Ex)/(Ob/Ex)_{max}] - 0.5$$

where Ob is the density of eels observed for the class, Ex is the expected density for a theoretical random distribution, and $(Ob/Ex)_{max}$ is the maximum value of (Ob/Ex) for the class. 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 three different size classes, we used the Wilcoxon non-parametric test (Z).

RESULTS

Population Structure

A total of 1774 European eels were sampled. The sizes varied from 60 mm to 790 mm; mean ± sd = 214 ± 108 mm (Figure 2). Total densities were between 0.0 eel.100 m^{-2} and 52.5 eels.100 m^{-2} (mean ± sd = 10.5 ± 11.0 eel.100 m^{-2}); however, eels <280 mm were much more abundant than eels >280 mm (Table 1, Figure 2). Depending on the sampling date, the eel frequency of occurrence (percentage of sampling sites where eels were present) varied between 70% and 100%.

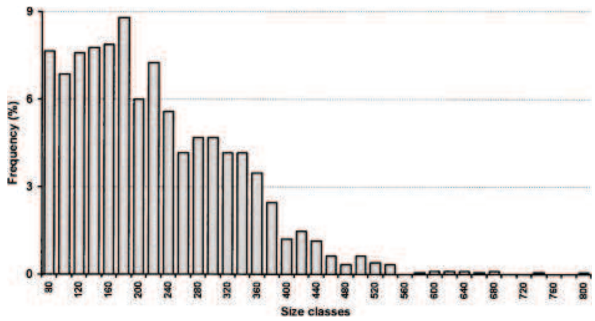

Figure 2. Length histogram (mm) of eels sampled (N = 1774 eels) in 141 stations of the marsh study between 1996 and 2000.

Table 1. Density of each eel size class in the study site (number of eels. 100 m^{-2}). Min: minimum density, Max: maximum density, Mean: mean density, sd: standard deviation. n: number of eels measured.

	Eel Size Classes			
	<160 mm	[160–240 mm]	[240–360 mm]	>360 mm
Min	0	0	0	0
Max	40	27	13	7
Mean	9.4	6.0	1.8	1.2
sd	10.0	5.4	2.4	1.7
n	630	671	297	176

The cluster analysis indicated that fish sorted into four size-class groups at the 60% probability level based on dissimilarities between size-class group abundance and samples (Figure 3): cluster A was composed of eels <160 mm; cluster B of eels between 160 and 240 mm; cluster group C of eels between 240 and 360 mm, and cluster D of eels >360 mm. These size classes correspond to different behaviors, especially in this reclaimed marsh, and according to this analysis to different habitat preferences (see ecological profiles). The first size class (<160 mm) represents recently recruited elvers, which have just started their colonization of the marsh system. The second class (between 160 and 240 mm) consists mainly of sedentary yellow eels. The two remaining stages (240–360 mm and >360 mm) reflect potential reproductive status represented by future male or female silver eels.

So, four ANN models were developed, one for each size class (<160, [160–240], [240–360], and >360 mm). We could have used a single neural network with four dependent variables (one for each of the four size classes), but we preferred four networks with the same architecture, each predicting the abundance of one size-class group. This allowed us to estimate the influence of the local environmental variables on each eel size class independently.

Model Fitting and Testing

According to the Pearson correlation matrix (with Bonferroni post-analysis) few of the habitat variables were significantly correlated with each other (all $r < 0.5$). The only significant relations were between floating-leaved plants and submerged plant beds ($r = 0.485$, $p < 0.001$) and between ditch width and water depth ($r = 0.463$, $p < 0.001$). Therefore, all microhabitat factors were included in the models.

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 (local environmental variable). The hidden layer had three neurons, determined as the optimal configuration, to give the lowest error in the training and testing sets of data. The output neuron computes the values of the dependent variables (eel densities according to size classes). A 'bias' neuron was added to each computational layer (i.e., hidden and output layer). These neurons had a constant input value of one and were used to lower biases in the modelling procedure.

The ANN models of 500 iterations (best compromise between bias and variance, which is quite low in ANN modelling) show that the correlation coefficient (r) between observed and predicted values of the dependent variable varied from 0.89 to 0.92 for training

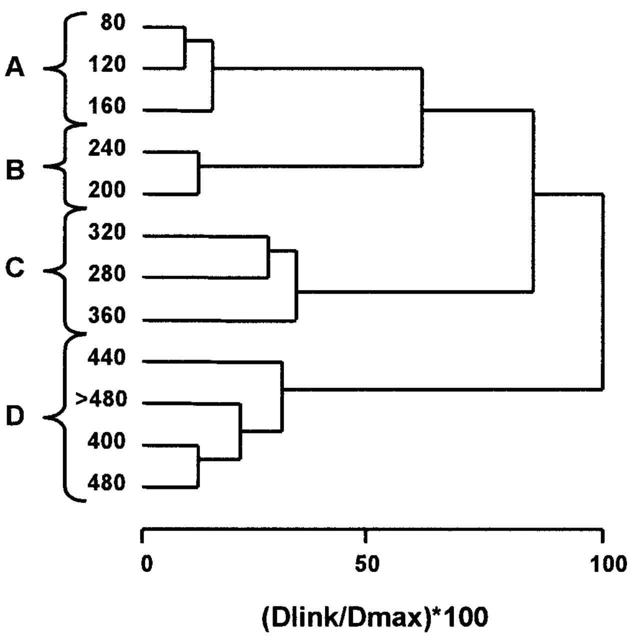

Figure 3. Cluster analysis (Ward's method, Euclidean distance) of eel size-class abundance. The linkage distance (Dlink) is presented as a percentage of the maximum linkage distance (Dmax). A, B, C, D: cluster groups. Numerical column (from 80 to 480) is eel length (mm).

Table 2. Correlation coefficient (r) between observed and estimated values in the artificial neural network (ANN) during training and testing for each eel size class.

	Eel Size Classes			
	<160 mm	[160–240 mm]	[240–360 mm]	>360 mm
r training	0.90	0.89	0.91	0.92
r testing	0.74	0.71	0.76	0.81

sets and from 0.71 to 0.81 for testing sets (Table 2). Relationships between residuals and values predicted by the model show that the correlation coefficients were negligible and not significant (r between 0.01 and 0.03, and p between 0.68 and 0.82 in both training and 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. The modelling procedure showed that eel densities were highly connected to two or three important influencing variables: the width of ditch section (contributions ranged from 11% to 52%, mean: 38%), the silt depth (from 27% to 35%, mean: 32%), and emergent plants (from 5% to 31%, mean: 16%). Except for floating plants for eels between 240 and 360 mm, other variables had a lower individual contribution (Table 3).

Ecological Profiles

The ecological profiles of the four size classes were only significantly different between eels >360 mm and eels <160 mm and between eels >360 mm and eels from 160 mm to 240 mm (Wilcoxon's non-parametric test, $Z = -2.343$, $p = 0.019$ and $Z = -2.296$, $p = 0.022$, respectively). In fact, the ecological profiles revealed no strong avoidance, except for high emergent vegetation for eels between 240 and 360 mm (Figure 4). Nevertheless, a number of tendencies were apparent: 1) All size classes except small eels avoided habitats with a high emergent aquatic vegetation cover. 2) Small eels (<160 mm) were found in every type of habitat (Figure 4A). 3) Eels of intermediate size class (160–240 mm and 240–360 mm) had very similar ecological profiles, but they were associated with larger ditches (widths >3 m) and silt depths <50 cm (Figure 4B and 4C). 4) The most significant differences concern larger eels (size class >360 mm); they were linked to wide ditches (widths >5 m) with water depths >80 cm, silt depth <30 cm and small quantities of aquatic plants (Figure 4D).

In summary, ecological profiles revealed that small eels were more widespread than large eels. Large size class were absent or scarce (low density) in shallow

Table 3. Percentage contribution of each independent variable to the prediction of eel densities according to eel size class obtained by partial derivatives (PAD).

	Eel Size Classes			
	<160 mm	[160–240 mm]	[240–360 mm]	>360 mm
Width	40.7	51.6	10.9	49.9
Water Depth	3.7	2.6	0.6	7.0
Silt Depth	26.8	35.3	34.4	30.5
Floating plants	5.9	2.8	21.3	0.9
Submerged plant	3.1	3.8	1.4	6.9
Emergent plant	21.3	6.9	31.4	4.8

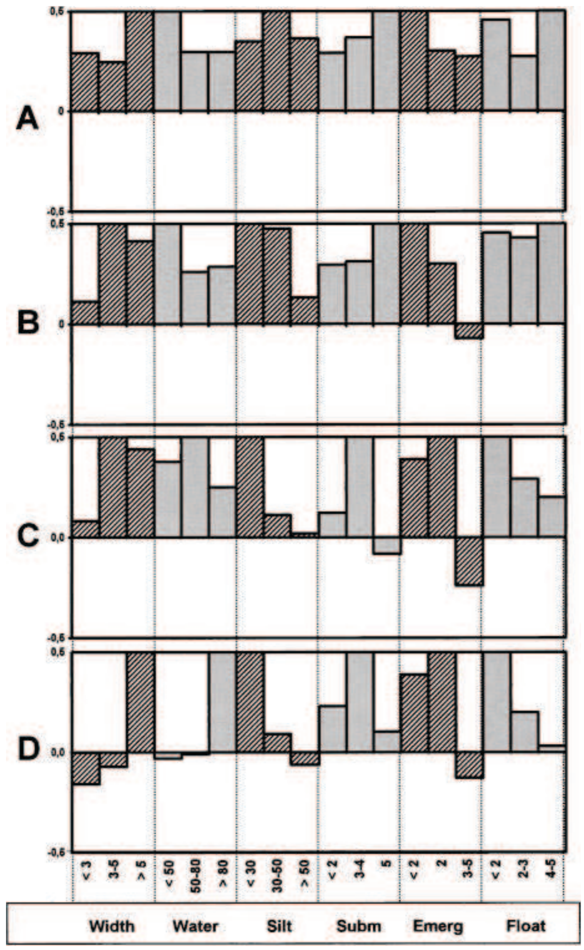

Figure 4. Microhabitat profile (axe Y) of three European eel size classes, <160 mm (A), [160 mm−240 mm] (B), [240 mm−360 mm] (C), and >360 mm (D) calculated for each environmental variable (axe X—see text for detail). Width: section width, Water: water depth, Silt: silt depth, Subm: submerged plant beds, Emerg: emergent plants on the bank of ditch and Float: floating-leaved plants.

ditches with a high cover of aquatic plants obstructing the water column. As a consequence, this analysis suggests a shift in habitat preference according to the eel size class, mainly for large eels >360 mm.

DISCUSSION

Capacity of the Predictive Model

In the context of defining the threshold size of the European eel stock (recommended by the ICES 1998), several studies have attempted to estimate the size of local stocks using various methods based on fishery surveys (Ardizzone and Corsi 1985), scientific surveys (Feunteun et al. 1998, Baisez 2001), or modelling (Dekker 2000). However, most of these studies did not take into account the characteristics of the available habitats and potential variations in habitat preferences of the eels according to size. However, preliminary studies in reclaimed marshes (Feunteun 1994, Baisez 2001) revealed surprising heterogeneity in the eel distribution, suggesting that such relationships may be important. Since the 1970s, studies have been conducted to describe the European eel spatial distributions in river systems (e.g., Naismith and Knights 1993, Lobon-Cervia et al. 1995, Feunteun et al. 1998, Laffaille et al. 2003) and lakes (e.g., Adam 1997). Most of these studies concluded that the species is ubiquitous. Knights et al. (2001) even concluded that no strong habitat index could be developed for European eels except a general decrease of abundance and increase of size from downstream to upstream reaches.

Smogor et al. (1995) underlined the difficulty of modelling American eel (*Anguilla rostrata* LeSueur) densities according to available habitat heterogeneity and eel size classes. In fact, these authors found that eel distribution differed with density in small coastal catchments: in catchments where eel density was very high, habitat associations were apparent, whereas in others, distance from the sea governed eel distribution. For example, Ibbotson et al. (2002) found that the negative relation with distance from the sea accounted for between 19 and 90% of the variation in European eel density in 18 UK rivers. Glova et al. (1998) arrived at a similar conclusion for the New Zealand eel species. However, Laffaille et al. (2003) developed a spatial organization model of European eel in a densely populated small catchment using ANN methodology. Our present study demonstrated that ANN models can provide a reliable prediction of the spatial distribution of an European eel population in a freshwater reclaimed marsh using simple microhabitat descriptors such as ditch width, water and silt depths, and vegetation cover. Given the success of the developed models, it is not unreasonable to combine density predictions with GIS approaches to identify and map habitat types with related density estimates and finally produce a quantification of the eel stock per size class across large areas (i.e., the whole catchment or the whole marsh system). Broad et al. (2001) have used this methodology to predict successfully the probabilities of occurrence of longfinned eel (*Anguilla dieffenbachii* Gray) in a New Zealand river.

Ecological Profiles

In a preliminary analysis, the abundance of the 'breton-vendéen' marsh's eel population seems high compared to other west European catchment (Moriarty and Dekker 1997, Feunteun et al. 1998). This is not surprising, given the situation in the Atlantic coastal marshes with respect to the arrival of European glass eels. Since at least the 1980s, the stocks have declined in the reclaimed marshes (Feunteun et al. 1999, Baisez et al. 2000).

It is generally believed that the distance to the sea is the most structuring parameter for the density, the average size, the age, and the sex ratio of European eels within a catchment area (e.g., Naismith and Knights 1993, Lobon-Cervia et al. 1995, Ibbotson et al. 2002). In reclaimed marshes, the strong space-time heterogeneity of the eel densities (Baisez et al. 2000) seems surprising since all the sampled sites are located less than 10 km from the sea and show relatively homogeneous characteristics compared to inland rivers (only one type of substrate, no water-velocity fluctuation, etc.). However, without taking into account the distance to the sea, some preferences by size classes were highlighted by this study. Firstly, the eels of size <160 mm seem to have a more ubiquitous behavior. Only deeper silt and dense aquatic vegetation seem to be unsuitable for this small size class. Secondly, the eels of intermediate sizes (between 160 mm and 360 mm) show a progressive change of habitat preference. These eel sizes prefer deeper habitats with less silt. Finally, the large eels (>360 mm) have a strong preference for large ditches with deep water, a thin silt layer, and low aquatic vegetation cover. The general pattern is for eels to shift progressively to deeper habitats as they grow. Similar to the observations of Glova et al. (1998) for *A. australis* (Richardson) and *A. dieffenbachii*, we found that this shift in behavior and habitat preferences occur around a size of 300 mm for European eels.

Consequently, small eels prevail in relatively narrow shallow ditches with significant vegetation where the larger sizes of eels are absent. These habitats are ditches poorly connected to the main river (Feunteun 1994, Baisez 2001). This type of distribution is relatively well-known. For example, Ford and Mercier (1986) showed that the small sizes of *Anguilla rostrata* prevail in the narrowest sections of salt marshes. Chisnall (1996) indicated that Australian eels (*A. australis*) of size <380 mm are primarily present around the edge of lakes. Neveu (1981) also showed a predominance of small sizes of European eel in shallow river habitats. Conversely, large eels dominate in the deeper sections of the marshes. Similar observations were made in large (Lamouroux et al. 1999) and small rivers (Laffaille et al. 2003). These results are also consistent with other studies that found that deeper habitats are the main feeding and resting sites for large eels (e.g., Glova 1988, Chisnall and Hicks 1993, Baisez 2001). According to Baisez (2001), these preferences seem to define the primary ditch network (main rivers) and secondary ditch network (directly connected to the primary network). Both secondary and primary networks are subject to regular maintenance (silt clearing) to prevent floods and to facilitate either drainage or irrigation of croplands.

Application for Conservation

Even if fish abundance and microhabitat use are strongly affected by underlying biotic interactions such as competition, predation, and resource limitation, the spatial assemblages of fish communities or populations are often related to environmental variables (Grossman et al. 1998, Laffaille et al. 2001, 2003). In the reclaimed marshes, it is not distance from the sea or other typical habitat variables that most strongly influence eel spatial organization, but mainly the synergy of three factors: ditch width, silt depth, and density of aquatic vegetation. These factors are related to the maintenance level of the ditches: the closest to the main river being the most regularly dredged and the most distant being rarely maintained. In turn, the narrowest and most silted-up ditches are less accessible and only available for moving eels belonging to the smallest size classes (Baisez 2001). As eels grow, they progressively leave these shallow habitats, which are then available for new recruits. For habitat maintenance or restoration, the difficulty is to assess what proportions of different habitat types are necessary to maintain an eel population according to production objectives (production of pre-spawners and fishery production).

The heterogeneity of each sampling station was generally defined according to a landscape connectivity descriptor of the ditch network and human management. The large and deep ditches, which correspond to the main rivers (ditches directly connected to the sea) and the secondary network (ditches directly connected to the river), are managed to maintain a low quantity of aquatic vegetation and silt. Analysis showed that the largest eels mainly colonized these areas, which are generally excavated every 5 to 10 years by collective management. The narrow and shallow ditches, connected to the secondary network, are more rarely managed by private landowners and are more often characterized by a high cover of submerged plants and greater silt depth. In these ditches representing about 85% of the total network length in the study area (Baisez 2001), only small sizes were observed before a clearing operation. So, the lowered frequency of dredging of this part of the ditch network (reductions observed since the 1970s) seems to have resulted in a decreased carrying capacity of the marsh for the largest eel sizes. On the other hand, the biological richness and diversity of these ecosystems are mainly correlated with the preservation of a diversity of silting stages among the ditch population. So, management of regular dredging operations in the channels by maintaining a mosaic of permanent aquatic habitats and avoiding the heavy silt loads in most ditches should be promoted.

The geographic setting of the Atlantic coastal marshes favors high European eel density (Baisez et al. 2000). Various methods of capture (fishing, extensive production in ponds, etc.) have been used since the creation of these systems (Feunteun 1994). This exploitation was, and is still in some areas, a justifying element for the regular management of marsh waters. The integrated management of these coastal wetlands and their resources is an increasingly commonly accepted objective. Many marshes have been restored for waterfowl conservation (Eybert et al. 1998, Lefeuvre et al. 2003), but habitat restoration is rarely used to restore eel stocks, despite the belief that habitat degradation is one of the causes of the population decline (see Feunteun 2002). According to Feunteun (2002), this is probably one of the most promising ways for restoring inland eel stocks. Better knowledge of habitat-eel relationships may contribute to this objective, as we have tried to demonstrate in this study.

ACKNOWLEDGMENTS

This study was a contribution of the 'Tableau de bord anguille du bassin de la Loire, des côtiers vendéens et de la Sèvre Niortaise'. The help of many colleagues of Cemagref Bordeaux and University of Rennes 1 was also indispensable in the fieldwork, thanks to them. We thank the anonymous reviewers for many helpful suggestions, and the Editor-in-Chief for his patience.

LITERATURE CITED

Adam, G. 1997. L'anguille européenne (*Anguilla anguilla* L. 1758): dynamique de la sous-population du lac de Grand-Lieu en relation avec les facteurs environnementaux et anthropiques. Ph. D. Dissertation. University of Toulouse 3, France.

Ardizzone, G. D. and F. Corsi. 1985. Eel population structure, dynamics and fishing yield in a Mediterranean coastal lagoon. Oebelia 11:547–560.

Baisez, A. 2001. Optimisation des suivis des indices d'abondances et des structures de taille de l'anguille européenne (*Anguilla anguilla*, L.) dans un marais endigué de la côte atlantique: relations espèce—habitat. Ph. D. Dissertation. University of Toulouse 3, France.

Baisez, A., C. Rigaud, and E. Feunteun. 2000. Hétérogénéité de répartition de l'anguille européenne (*Anguilla anguilla*, L.) observée par pêche électrique dans un marais endigué de la côte atlantique française (Marais breton). Cybium 24:23–32.

Beecher, H. A., T. H. Johnson, and J. P. Carleton. 1993. Predicting microdistributions of steehead (*Oncorhynchus mykiss*) parr from depth and velocity preference criteria: test of an assumption of the instream flow incremental methodology. Canadian Journal of Fisheries and Aquatic Sciences 50:1380–1387.

Beja, P. R. 1996. Seasonal breeding and food resources of otters, *Lutra lutra* (Carnivora, Mustelidae), in South-West Portugal: a comparison between coastal and inland habitats. Mammalia 60: 27–34.

Broad, T. L., C. R. Townsend, C. J. Arbuckle, and D. J. Jellyman. 2001. A model to predict the presence of longfin eels in some New Zealand streams, with particular reference to riparian vegetation and elevation. Journal of Fish Biology 58:1098–1112.

Brosse, S., P. Laffaille, S. Gabas, and S. Lek. 2001. Is scuba sampling a relevant method to study fish microhabitat in lakes? Examples and comparisons for three European species. Ecology of Freshwater Fish 10:138–146.

Butet, A. and A. B. Leroux. 2001. Effects of agriculture development on vole dynamics and conservation of Montagu's harrier in western French wetlands. Biological Conservation 100:289–295.

Carle, F. L. and M. R. Strub. 1978. A new method for estimating population size from removal data. Biometrics 35:621–630.

Chisnall, B. L. 1996. Habitat associations of juvenile shortfinned eels (*Anguilla australis*) in shallow lake Waahi, New Zealand. New Zealand Journal of Marine and Freshwater Research 30:233–237.

Chisnall, B. L. and B. J. Hicks. 1993. Age and growth of longfinned eels (*Anguilla dieffenbachii*) in pastoral and forested streams in the Waikato river basin and in two hydro-electric lakes in the North island, New Zealand. New Zealand Journal of Marine and Freshwater Research 27:317–332.

Colasanti, R. L. 1991. Discussions of the possible use of neural network algorithms in ecological modelling. Binary 3:13–15.

Cowx, I. G. 1983. Review of the methods for estimating fish population size from survey removal data. Fisheries Management 14: 67–82.

Dekker, W. 2000. A Procrustean assessment of the European eel stock. ICES Journal of Marine Science 57:938–947.

Dimopoulos, I., J. Chronopoulos, A. Chronopouls-Sereli, and S. Lek. 1999. Neural networks models to study relationship between lead concentration in grasses and permanent urban descriptors in Athens city (Greece). Ecological Modelling 120:157–165.

Efron, B. 1983. Estimating the error rate of a prediction rule: some improvements on cross-validation. Journal of the American Statistical Association 78:316–331.

Eybert, M.-C., J. Y. Bernard, P. Constant, E. Feunteun, J. Hedin, and S. Questiau. 1998. Réhabilitation des prairies inondables dans les marais Briérons: évolution de la flore, des poissons et des oiseaux. Gibier Faune Sauvage 15:999–1016.

Feunteun, E. 1994. Le peuplement piscicole du marais littoral endigué de Bourgneuf-Machecoul (France, Loire-Atlantique). Approche méthodologique pour une analyse quantitative de la distribution spatiale du peuplement piscicole et de la dynamique de certaines de ses populations. Ph. D. Dissertation. University of Rennes 1, France.

Feunteun, E. 2002. Management and restoration of the European eel population (*Anguilla anguilla*): an impossible bargain? Ecological Engineer 18:575–591.

Feunteun, E., A. Acou, J. Guillouët, P. Laffaille, and A. Legault. 1998. Spatial distribution of an eel population (*Anguilla anguilla* L.) in a small coastal catchment of Northern Brittany (France). Consequences of hydraulic works. Bulletin Français de la Pêche et de la Pisciculture 349:129–139.

Feunteun, E., A. Acou, P. Laffaille, and A. Legault. 2000. The European eel: prediction of spawner escapement from continental population parameters. Canadian Journal of Fisheries and Aquatic Sciences 57:1627–1635.

Feunteun, E., C. Rigaud, and P. Elie. 1992. Le marais doux endigué de Bourgneuf-Machecoul: premiers éléments de connaissance du peuplement piscicole, relation ichthyofaune habitat, mise en évidence des problèmes majeurs de gestion. Revue des Sciences de l'Eau 5:509–527.

Feunteun, E. and L. Marion. 1994. Impact of heron (*Ardea cinerea*) on fish communities: the case study of the main European colony. Hydrobiologia 279/280:327–344.

Feunteun, E., C. Rigaud, P. Elie, and J.-C. Lefeuvre. 1999. Les peuplements piscicoles des marais littoraux endigués atlantiques: un patrimoine à gérer? Le cas du marais de Bourgneuf Machecoul (Loire-Atlantique, France). Bulletin Français de la Pêche et de la Pisciculture 352:63–79.

Ford, T. E. and E. Mercer. 1986. Density, size distribution and home range of American eels, *Anguilla rostrata*, in a Massachusetts salt marshes. Environmental Biology of Fishes 17:309–314.

Fustec, E. and J.-C. Lefeuvre (eds.). 2000. Fonctions et valeurs des zones humides, Dunod, Paris.

Gevrey, M., I. Dimopoulos, and S. Lek. 2003. Review and comparison of methods to study the contribution of variables in artificial neural networks models. Ecological Modelling 160:249–264.

Giske, J., G. Huse, and O. Fiksen. 1998. Modelling spatial dynamics of fish. Reviews in Fish Biology and Fisheries 8:57–97.

Glova, G. J. 1988. Fish density variations in the braided Ashley River, Canterbury, New Zealand. New Zealand Journal of Marine and Freshwater Research 22:9–15.

Glova, G. J., D. J. Jellyman, and M. L. Bonnet. 1998. Factors associated with the distribution and habitat of eels (*Anguilla* spp.) in three New Zealand lowland streams. New Zealand Journal of Marine and Freshwater Research 32:255–269.

Grossman, G. D., R. E. Ratajczak, M. Crawford, and M. C. Freeman. 1998. Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. Ecological Monograph 68:395–420.

Guisan, A. and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147–186.

Ibbotson, A., J. Smith, P. Scarlett, and M. Aprhamian. 2002. Colonisation of freshwater habitats by the European eel *Anguilla anguilla*. Freshwater Biology 47:1696–1706.

ICES. 1998. European eel. Extract of the report of the ICES Advisory Committee on Fishery Management. International Council for the Exploration of the Sea, Copenhagen, Denmark.

ICES. 1999. European eel. Extract of the report of the ICES Advisory Committee on Fishery Management. International Council for the Exploration of the Sea, Copenhagen, Denmark.

ICES. 2002. European eel. Extract of the report of the ICES Advisory Committee on Fishery Management. International Council for the Exploration of the Sea, Copenhagen, Denmark.

Ivlev, V. S. 1961. Experimental Ecology of the Feeding of Fishes. Yale University Press, New Haven, CT, USA.

Knights, B., A. Bark, M. Ball, F. Williams, E. Winter, and S. Dunn. 2001. Eel and elver stocks in England and Wales. Status and management options. Environment Agency, UK. R&D Technical Report W248.

Kohavi, R. 1995. A study of the cross-validation and bootstrap for accuracy estimation and model selection. p. 1137–1143. *In* Proceeding of the Intelligence Joint Conference on Artificial Intelligence, Montreal, Quebec, Canada.

Laffaille, P., S. Brosse, S. Gabas, and S. Lek. 2001. Fish spatial distribution in the littoral zone of Lake Pareloup (France) during summer. Archiv für Hydrobiologie 153:129–144.

Laffaille, P., E. Feunteun, A. Acou, and J.-C. Lefeuvre. 2000b. Role of European eel (*Anguilla anguilla* L.) in the transfer of organic matter between marine and freshwater systems. Verhandlungen Internationale Vereinigung für Limnologie 27:616–619.

Laffaille, P., E. Feunteun, A. Baisez, T. Robinet, A. Acou, A. Legault, and S. Lek. 2003. Spatial organisation of European eel (*Anguilla anguilla* L.) in a small catchment. Ecology of Freshwater Fish 12:254–264.

Laffaille, P., J.-C. Lefeuvre, and E. Feunteun. 2000a. Composition of fish communities in macrotidal salt marshes of the Mont Saint-Michel bay (France). Estuarine, Coastal and Shelf Science 51: 429–438.

Lamarque, P. J., J. Arignon, and C. Gosset. 1978. Comparaison des appareils de pêche à l'électricité EPMC et Héron. Bulletin Français de pêche et de Pisciculture 270:223–236.

Lambert, P., E. Feunteun, and C. Rigaud. 1994. Eel study in freshwater marshes. First analysis of catch probability observed during electric fishing operations. Bulletin Français de la Pêche et de la Pisciculture 335:111–122.

Lamouroux, N., H. Capra, M. Pouilly, and Y. Souchon. 1999. Fish habitat preferences in large streams of southern France. Freshwater Biology 42:673–687.

Lefeuvre, J.-C., P. Laffaille, E. Feunteun, V. Bouchard, and A. Radureau. 2003. Biodiversity in salt marshes: from the patrimonial value to the ecosystem functioning. The case study of the Mont Saint-Michel bay. Comptes Rendus Biologies 326:125–131.

Legault, A. 1994. Etude préliminaire du recrutement fluvial de l'anguille. Bulletin Français de la Pêche et de la Piscicultur 335: 33–42.

Lek, S. and J. F. Guégan. 1999. Artificial neural networks as a tool in ecological modelling, an introduction. Ecological Modelling 120:65–73.

Lobon-Cervia, J., C. G. Utrilla, and P. A. Rincon. 1995. Variations in the population dynamics of the European eel *Anguilla anguilla* (L.) along the course of a Cantabrian river. Ecology of Freshwater Fish 4:17–27.

Marion, L. and L. Brient. 1998. Wetland effects on water quality: input-output studies of suspended particulate matter, nitrogen (N) and phosphorus (P) in Grand-Lieu, a natural plain lake. Hydrobiologia 373/374:217–235.

Moriarty, C. and W. Dekker (eds.). 1997. Management of European Eel Fisheries. Irish Fishery Bulletin 15.

Naismith, I. A. and B. Knights. 1993. The distribution, density and growth of the European eel, *Anguilla anguilla*, in the freshwater catchment of the River Thames. Journal of Fish Biology 42:217–226.

Nelva, A., H. Persat, and D. Chessel. 1979. Une nouvelle méthode d'étude des peuplements ichtyologiques dans les grands cours d'eau par échantillonnage ponctuel d'abondance. Comptes Rendus de l'Académie des Sciences III, Life Sciences 289:1295–1298.

Neveu, A. 1981. Density and microdistribution of the various fish species in Lower Nivelle, a small coastal river in Pyrénées Atlantiques. Bulletin Français de la Pêche et de la Pisciculture 280:86–102.

Rigaud, C., J. Massé, A. Dutartre, and V. Merle. 1996. Programme Life/Norspa 'Baie de Bourgneuf et Marais bretons'. Volet 'Restauration du réseau secondaire du marais doux'. Report Cemagref, Bordeaux, France.

Rumelhart, D. E., G. E. Hinton, and R. J. Williams. 1986. Learning representations by back-propagation error. Nature 323:533–536.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape area? Biological Conservation 83:247–257.

Smogor, R. A., P. L. Angermeier, and C. K. Gaylord. 1995. Distribution and abundance of American eels in Virginia streams: tests of null models across spatial scales. Transactions of the American Fisheries Society 124:789–803.

Manuscript received 17 March 2003; revisions received 29 March 2004 and 10 May 2004; accepted 1 June 2004.