Temporal patterns in the upstream migration of European glass eels (*Anguilla anguilla*) at the Couesnon estuarine dam

P. Laffaille [a,*], J.-M. Caraguel [b], A. Legault [b]

[a] *Equipe de Recherche Technologique 52 «Biodiversité Fonctionnelle et Gestion des Territoires», Université de Rennes 1, Campus de Beaulieu, 35042 Rennes cedex, France*

[b] *Fish Pass, 8 allée de Guerlédan, Z.A. Parc rocade sud, 35135 Chantepie, France*

Abstract

The temporal migration patterns of European glass eel *Anguilla anguilla* at the Couesnon estuarine dam (Mont-Saint-Michel Bay, France) were examined in winter and spring 2004 and 2005. The dam which is located close to the river mouth constitutes a major obstacle for upstream-migrating glass eels. The migration was observed at different temporal scales, from within individual tides to complete tidal cycles between successive spring tides. The maximum number of glass eels arrived downstream of the dam at the beginning and in the middle of the flood tide. Glass eels migrated through the dam openings preferentially from the middle of the flood to the beginning of the ebb tide. Eel densities were highest during the second tide of each tide cycle that arrived at the estuarine dam and when the difference in water level between upstream and downstream of the dam was greatest, particularly at the end of the flood. Analysis of the influence of each environmental factor provided a good prediction of the glass eel recruitment peaks and, therefore, of the most favourable temporal windows for their migration. The water level and temperature were the most important environmental factors. These results provide the information needed for a dam-management program that is compatible with glass eel migration.

Keywords: European eel; catadromy; hydraulic work; management; dam

1. Introduction

The European eel (*Anguilla anguilla* L.) is catadromous and has a long and complex life history cycle. Eels' spawn in the Sargasso Sea and the Gulf Stream distributes the leaf-like leptocephalus larvae along the Atlantic coasts of North Africa and Europe. The larvae metamorphose into glass eels in continental shelf waters and migrate inshore to coastal waters, estuaries and streams, where they become pigmented elvers and later yellow juvenile eels (Tesch, 2003). Eels are plastic in their choice of habitat, whether marine, estuarine, or freshwater (Daverat et al., 2006). Some glass eels and elvers stay in salt or brackish water along the coast while others penetrate rivers and streams to complete the growth stage in freshwaters. In France, the mid-latitude area of the European distribution, the beginning of glass eel recruitment in estuaries occurs in September (Elie and Rochard, 1994). Although recruitment occurs throughout the year, the main period is in winter, especially in the Mont-Saint-Michel Bay (Laffaille et al., 2000a). Studies of the timing of European glass eel migration have shown a two-stage sequence: (1) glass eels migrate upstream using the tidal currents via selective tidal stream transport (STST), allowing transport from the continental slope to estuaries at the least energy cost, and (2) when the water temperature reaches 10−12 °C, the glass eels swim actively upstream in the estuary (Gascuel, 1986; Beaulaton and Castelnaud, 2005). The first sequence is the beginning of the colonization process of the estuaries and the second one is for the whole freshwater system. Thus, the movements of glass eels into

* Corresponding author.
E-mail address: pascal.laffaille@univ-rennes1.fr (P. Laffaille).

doi:10.1016/j.ecss.2006.12.011

estuaries are essentially passive during the flood tide, by using the tidal current principally at night and hiding in the substrate during the ebb tide and the daytime (Gascuel, 1986; Elie and Rochard, 1994).

The European eel is an important resource in conservation, ecological and socio-economic terms (Baisez and Laffaille, 2005). The importance of glass eels has led to the recruitment of this migrating stage and its associated environmental factors being given considerable attention from researchers over many years (Elie and Rochard, 1994). The most important environmental factors that influence glass eel migration include: water temperature, lunar phase, discharge, tidal cycle, water conductivity, salinity, and water clarity (see for example, Ciccotti et al., 1995; White and Knights, 1997; De Casamajor et al., 1999; Jellyman and Lambert, 2003; Jessop, 2003; Bardonnet et al., 2005; Edeline et al., 2005). Moreover, the importance of the environmental factors affecting glass eel migration differs according to location, estuary characteristics and physiological status of the eels (Elie and Rochard, 1994).

Since the 1980s, the abundance of the European eel has declined throughout its distribution range (Moriarty and Dekker, 1997; Dekker, 2003). ICES recently recommended that all means should be taken to restore the depleted stocks, at all biological stages. A stock recovery plan is urgently needed (ICES, 1999) including sustainable management (Rosell et al., 2005) and an eel report card (Baisez and Laffaille, 2005). Over-exploitation, changes in oceanographic conditions, pollution, parasitism, degradation of freshwater habitats, and reductions in the area of accessible freshwater habitat are some of the factors proposed for the decline (see for example Moriarty and Dekker, 1997; Feunteun, 2002; Dekker, 2003; Kirk, 2003). Russell and Potter (2003) have suggested that the principles of the precautionary approach are directly relevant to the management of European eel stocks. The application of this approach should relate to fishery and non-fishery factors such as the management of freshwater, estuarine and coastal habitats. A number of attempts could be made to manage freshwater habitat availability, such as management of physical obstructions to migration (Legault, 1988; Knights and White, 1998; Briand et al., 2005a). Dam construction has been identified as a major factor responsible for the severe reduction of freshwater eel stocks (Moriarty and Dekker, 1997; Feunteun, 2002). In fact, like the Couesnon River (Mont-Saint-Michel Bay, France), a number of European estuaries are obstructed by barriers or dams (see for example Briand et al., 2003; Briand et al., 2005a). In the estuaries, selective tidal stream transport (STST) will concentrate glass eels at a point, defined by tidal and river currents, where STST is no longer effective (Gascuel, 1986). But, during this upstream migration, glass eels are stopped in estuaries by physical barriers such as dams (Legault, 1990; Laffaille et al., 2000b; Briand et al., 2003). Because the behaviour of glass eels leads them to congregate near to a dam, the efficiency of professional and angler fishing may be sufficiently high to deplete the local stock in dammed estuaries (Briand et al., 2003).

With the substantial decline in recruitment recorded for *Anguilla anguilla*, and the number of estuaries obstructed by dams, there is renewed importance in the timing and environmental conditions associated with recruitment of glass eels in obstructed estuaries. The aim of this study in the Couesnon estuary was, therefore, to determine the temporal migration dynamics of glass eels in an obstructed estuary, so that management options for eel passage at estuarine dams could be developed.

2. Materials and methods

2.1. Study site

The Couesnon is a small river with a catchment area of 1120 km^2 that forms the boundary between Brittany and Normandy (France). The estuary is situated in the Mont-Saint-Michel Bay (Fig. 1). The Mont-Saint-Michel Bay is an extensive coastal zone (latitude 48°40′ N, longitude 1°35′ W) extending over 500 km^2. This area is a macrotidal system characterized by a high tidal range (mean tidal range = 10–11 m, maximum 16 m) and high difference between neap and spring tides (about 10 m) that depends mainly on the lunar cycle, wind orientation, and atmospheric pressure.

An estuarine dam (20 m long), fitted with automatic tide gates, controls flows and protects housing estates in the

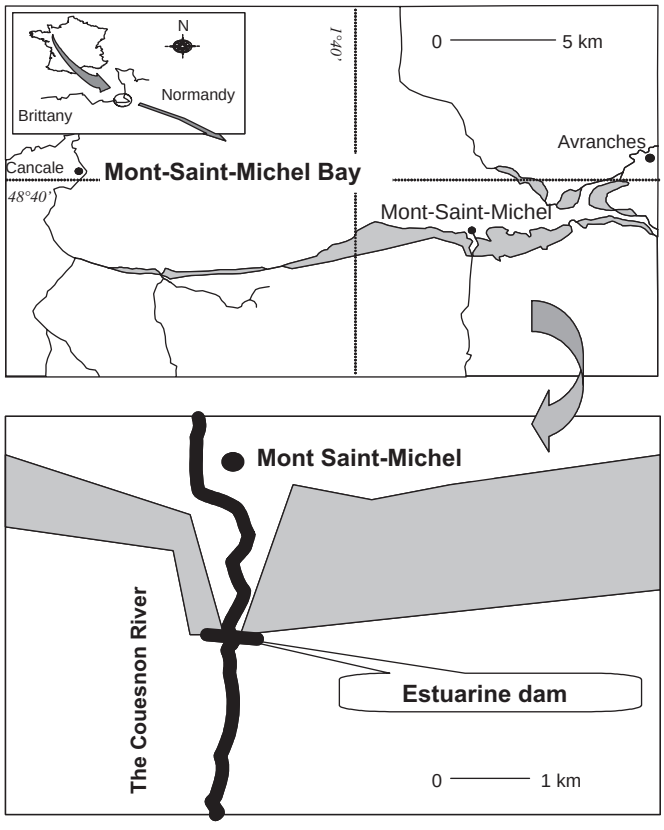

Fig. 1. Map of the study site showing location of Mont-Saint-Michel Bay, the Couesnon River and the estuarine dam. The grey hatching represents the salt marshes.

Couesnon estuary. The sea arrives at the dam during spring tides. During the flood tide, the passive floodgates stop the tide and the water levels downstream of the dam gradually increase continually until the tide starts to recede. During the present study, the mean duration of this phase was 70 min (SD = 10 min). During the ebb, water level decreases downstream of the dam but the floodgates remain closed until water levels upstream and downstream of the dam are similar. During the study, the mean duration of this phase was 106 min (SD = 19 min). It is only when water levels downstream of the dam are below upstream levels that the Couesnon River flow can push the gates open and water can once again flow freely downstream. However, glass eels could not swim upstream during this ebb tide period when the tidal gates were open. In fact, the majority of glass eels are in the passive migration phase, and during this phase, glass eels migrate upstream only using the tidal currents via selective tidal stream transport (Gascuel, 1986; Lambert et al., 2003).

This hydraulic barrier, situated in the estuary near the river mouth, significantly reduces the possibility of colonization of the estuary and upstream freshwater habitats by marine and amphihaline fishes (Laffaille et al., 2000b). Because this type of estuarine dam completely stops the tide, it prevents glass eels from using tidal currents to colonize the estuary (Legault, 1990). However, two horizontal openings at the dam bottom (0.4 m × 6.4 m and 0.4 m × 0.6 m) that are very small compared to the dam size (20 m long) do allow a small portion of the tidal flow to enter the Couesnon River. These openings are always available for eels at the same width for all tides that arrive from the sea at the dam. There is little attractant freshwater flow passing through the openings, because the opening widths are small and the river flow is very small compared to the tidal flow. At no point during the study was there sufficient flow in Couesnon River to cause water levels upstream of the gates to be higher than downstream levels during an incoming tide. Consequently, glass eels could, therefore, pass through the dam when the gates are shut. On average, during the present study this potential access route was available for about 180 min (SD = 29 min).

2.2. Sampling method

Glass eels were caught during 58 spring tides: 31 from January to April 2004 and 27 from February to April 2005. Two horizontal plankton nets (0.4 m^2 cross-section, 0.8 mm mesh size) associated with the flood current were used to catch glass eels. One net was set downstream of the dam to catch eels that arrived from the sea (protocol 1) and the other placed upstream of the dam to determine numbers that passed through the openings in the gates (protocol 2). Both nets were set from the time the tide reached the gates (and consequently closed them) until water levels on either side of the gate were equal and the gates began to re-open. Differences in water level downstream and upstream of the dam associated with the flood current were continually measured to estimate the volume of water passing through the two openings in the dam.

The following temporal fluctuations in population abundances were determined using protocol 2: (1) The tidal cycle (seasonal variation) − by determining variation in catches between January and April (14 tidal cycles); (2) within tidal cycles (series of five successive tides in each cycle with different tidal ranges) − by sampling through three tide cycles in February 2004, March 2004 and February 2005; (3) diurnal − by separating day and night catches obtained on 14 occasions (two tide cycles of similar amplitude per day); (4) and within tides − by separating catches obtained at the beginning, middle, and end of the flood and ebb. The variation within tides was studied using protocol 1. Consequently, all "types" of tides occurring downstream the dam were taken into account. On each sampling occasion, records of water level (m), temperature (°C), salinity (practical salinity units) and turbidity (NTU) were obtained at 10-min intervals. A cloud cover index (0 = clear to 5 = 100% cover) and lunar phase period (1 = new moon to 15 = full moon) were also obtained.

2.3. Glass eel analyses

Glass eels were measured to the nearest 1 mm (total length, TL). Eel stages were identified from stage V to VII according to Elie et al. (1982). The glass eel to elver phase covers stages VA with no pigmentation except a spot on the caudal fin, VB with the early development of pigmentation on the skull and VIA0 with development of pigmentation along the base of dorsal fin and with the first pigment cells beyond the skull spot. The next stages are based on the development of surface and branchiostegal pigmentation.

2.4. Statistical analyses

Glass eel migration patterns were analyzed independently at different temporal scales. Densities were log $(x + 1)$ transformed to stabilize variance and normalize the distribution. This assumption was tested using Kolmogorov−Smirnov's method (Lilliefors option). Densities were then tested using parametric tests (one-way and repeated measures Anova with Tukey post-tests, unpaired and paired *t*-tests, and Pearson's *r*).

The influence of environmental factors on glass eel density was estimated using artificial neural network (ANN) techniques (see review of Lek and Guégan, 1999). We used one of the principles of ANN, the back-propagation algorithm (Rumelhart et al., 1986). The network was trained using an error back-propagation training algorithm. This algorithm adjusts the connection weights according to the back-propagated 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 modeling 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 jackknife 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). This step was used to assess the prediction capacity of the network.

The ANN used was a three-layered (6-3-1), feed-forward network with bias. Six input neurons coded the six independent variables (environmental factors that were tested for their influence on glass eel densities: sea level, sea temperature, water salinity, water turbidity, cloud cover and lunar phase). 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 (glass eel densities). 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 modeling procedure. 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 compared to other methods used to determine the sensitivity of independent variables (Gevrey et al., 2003).

Finally, we used scatter plots to display the relationships between glass eel densities and the main explicative variables using the PaD method. To obtain maximum ecological reliability, data fitting was performed with a LOWESS (Locally Weighted regression Scatter plot Smoothing) non-parametric regression model, which is known to reliably fit data tendencies and to respect the natural non-linearity of data (Trexler and Travis, 1993). We used the LOWESS smoothing function with $f = 0.80$. The f-value indicates the proportion of samples fitted by the LOWESS smoother; f varies between 0 and 1 according to the sensitivity of the analysis, with low values being more sensitive to local variation. The f-value is determined empirically by testing various possibilities and selecting the one which provides the best ability to visualise general data trends.

3. Results

3.1. Glass eel population structure

Of the 14 922 eels caught (6637 in 2004 and 8285 in 2005), only eight eels (80−166 mm) were not at the glass eel stage but were elvers (eel stage VII according to Elie et al., 1982) or young yellow eels. Throughout the sampling campaign, nine eel stages were observed from VA to VII, but 75% of eels were in the VB stage. Of the glass eels, the total length ranged from 55 to 82 mm (average ± SD = 69 ± 3.8 mm and 0.29 ± 0.06 g) and 70% of glass eels ranged from 65 to 72 mm. There are very little differences in length whatever the temporal variable taken into account (i.e., seasons, tide levels…).

3.2. Influence of the numbers of glass eels downstream of the dam

The densities of glass eels (mean ± SD) caught downstream of the dam (0.26 eels $m^{-3} \pm 0.17$ in 2004 and 0.18 eels $m^{-3} \pm 0.19$ in 2005) were about twofold higher than the densities of glass caught upstream of the dam (0.14 eels $m^{-3} \pm 0.26$ in 2004 and 0.09 eels $m^{-3} \pm 0.08$ in 2005) and differed significantly (paired t-test, $t = 3.94$, $p < 0.01$ in 2004 and $t = 3.21$, $p < 0.001$ in 2005). Glass eel densities at the top of the dam increased linearly with densities downstream of the dam ($r = 0.88$, $p < 0.001$; Fig. 2). However, upstream glass eel densities increased more slowly than downstream densities, and consequently a larger increase in downstream densities led to a small proportion of upstream passage.

3.3. Tide cycle variations

Seasonal variations of glass eel densities indicated that there were different periods (one-way Anova, $F = 5.52$, $p = 0.002$, Tukey post-test). Glass eel densities were lowest at the end of February (0.06 eels m^{-3} in 2004 and 0.02 eels m^{-3} in 2005) when the water temperature was lowest at between 2 and 4 °C (Fig. 3). The water temperature increased rapidly just before the highest glass eel densities that reached a peak at the end of March (0.40 eels m^{-3} in 2004 and 0.23 eels m^{-3} in 2005). This trend also showed that glass eel migration started before January, and certainly in the middle of December. Glass eel migration does occur in December when water temperatures were relatively high, around 7 °C (authors' unpublished data).

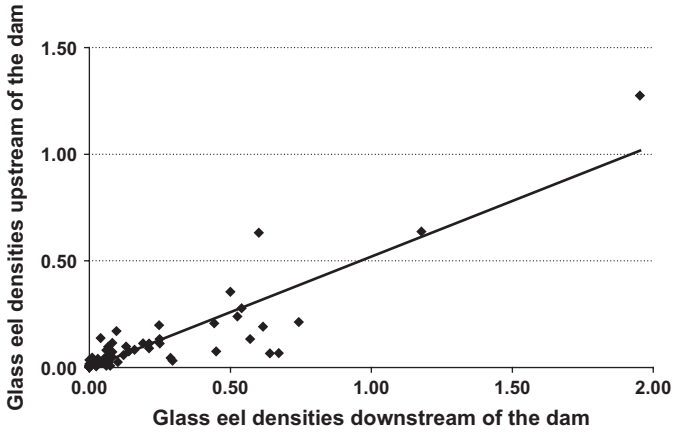

Fig. 2. Correlation between glass eel densities (number of eels per m^3) caught downstream of and upstream of the Couesnon dam in 2004 and 2005.

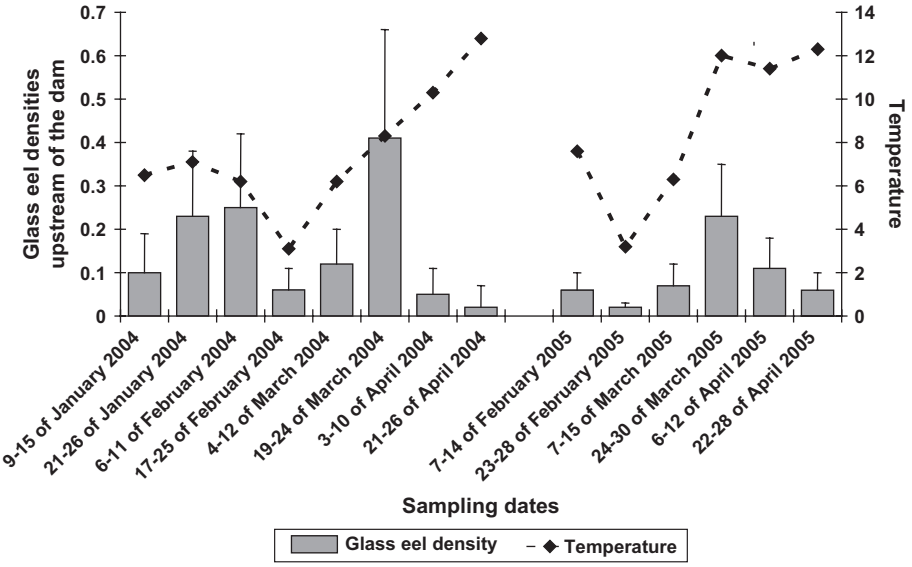

Fig. 3. Glass eel densities (number of eels ± SD per cubic meter) caught upstream of the Couesnon dam and mean water temperature (°C) during the 14 tidal cycles sampled in 2004 and in 2005.

3.4. Variations within the tidal cycle

The density of glass eels differed according to the five successive tides with different tidal amplitudes during the three tidal cycles (Anova for repeated data, $F = 7.91$, $p = 0.007$, Tukey post-test). About 10% of the total glass eel densities present during each tide cycle colonized the Couesnon upstream of the dam during the first tide that arrived downstream of the dam (Fig. 4). Moreover, the glass eel density was not greatest during the highest tidal amplitude, whatever the tide cycle. Densities were highest (about 50% of the total eel density during each tide cycle) only during the second tide after the sea arrived at the dam. Glass eel densities decreased regularly after this tide.

3.5. Daily variations during a tidal cycle

There were no significant differences in glass eel densities between morning and evening tides (paired student t-test, $t = 0.08$, $p = 0.935$).

3.6. Within tide variations

The densities of glass eels downstream of the dam differed (Anova for repeated data, $F = 7.85$, $p < 0.001$, Tukey post-test) according to the tidal stages (beginning, middle and end of flood and ebb periods). Glass eel arrival peaked (about 50% of the total density during each tide) at the beginning and the middle of the flood tide (Fig. 5). From the end of the flood

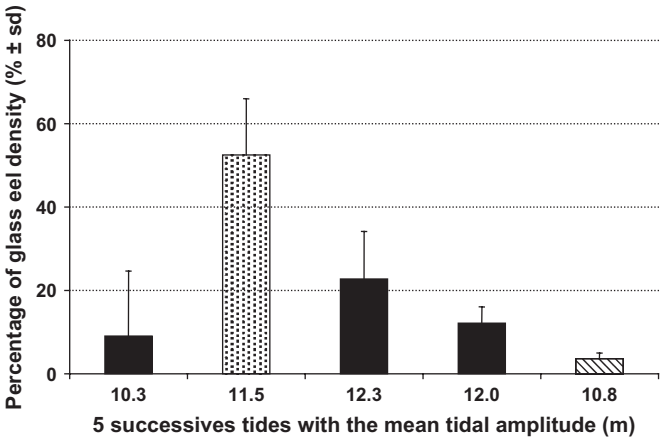

Fig. 4. Variations in the percentage (% ± SD) of glass eel densities caught upstream of the dam during five successive tides (with mean tidal amplitude) of three tidal cycles. Differences in shading indicate statistically significant differences.

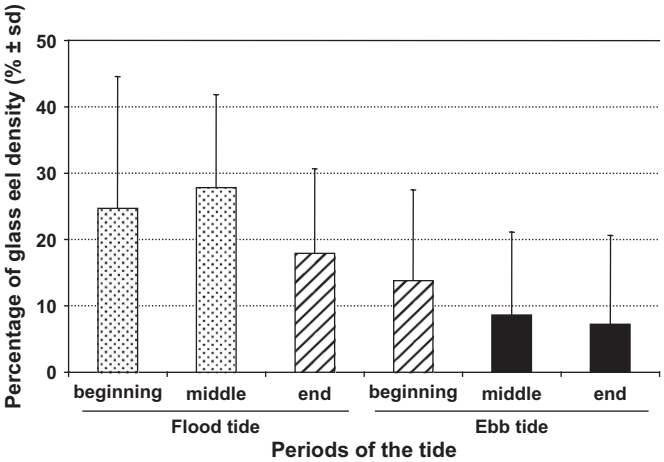

Fig. 5. Variations in the percentage (% ± SD) of glass eel densities caught downstream of the dam during the tide from the beginning of the flood to the end of the ebb. Differences in shading indicate statistically significant differences.

to the beginning of the ebb, the quantity of glass eel decreased (about 30% of the total density) and a small quantity was caught between the middle and the end of the ebb (less than 20% of the total density).

Similarly, there were differences in the intensity of glass eel migration through the Couesnon dam openings during the tide (Anova for repeated data, $F = 11.43$, $p < 0.001$, Tukey post-test). At the beginning of the flood tide about 10% of the total glass eel density during each tide migrated through the dam openings (Fig. 6). The period from the middle flood to the beginning of the ebb tide corresponded to the highest sea level at each tide. This was the preferential migration time (that corresponded to the point during the tide when the largest numbers of eels passed through the opening in the dam) when more than 65% of the total glass eel density during each tide migrated. The period from the middle to the end of ebb tide saw the proportion of glass eel densities that migrated through the dam openings decrease and become about 5% at the end of the tide.

3.7. Model fitting and testing

The ANN models of 500 iterations (best compromise between bias and variance, which is quite low in ANN modeling) show that the Pearson correlation coefficient (r) between observed and predicted values of the dependent variable was 0.87 for training sets and 0.84 for testing sets.

The PaD results that emphasize the relative contribution of the independent variables to the ANN models, showed that glass eel densities were highly connected to two important influencing environmental variables: the water temperature and secondly the sea level. The contributions of these two factors were more than 81%. Other variables had a lower individual contribution (Table 1). The general trend (LOWESS smoothing function) of glass eel density in relation to estuary water temperature showed that densities increased as water temperature increased from 3 to 9 °C and slightly decreased

Table 1
Data range and percentage contribution of each environmental factor used to predict glass eel densities. Contributions were obtained by partial derivation (PaD)

Factors	Data range	Contribution (%)
Sea temperature (°C)	2−15	58
Sea level (m)	9.8−12.7	23
Lunar phase index	1−15	7
Water turbidity (NTU)	5−780	5
Water salinity	0−30	4
Cloud cover index	0−5	3

at temperatures from 9 to 14 °C (Fig. 7A). Relationships between glass eel density and sea level showed the same tendency: the density increased rapidly as sea level increased to 12 m and decreased thereafter (Fig. 7B). Glass eel densities

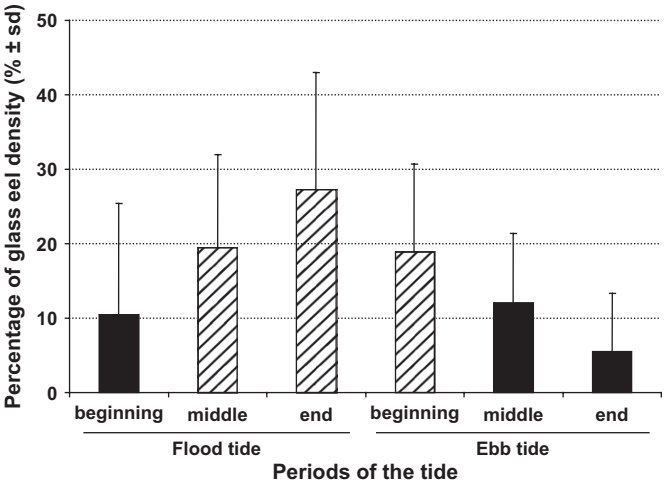

Fig. 6. Variations in the percentage (% ± SD) of glass eel densities caught upstream of the dam during the tide from the beginning of the flood to end of the ebb. Shading differences indicate statistically significant differences.

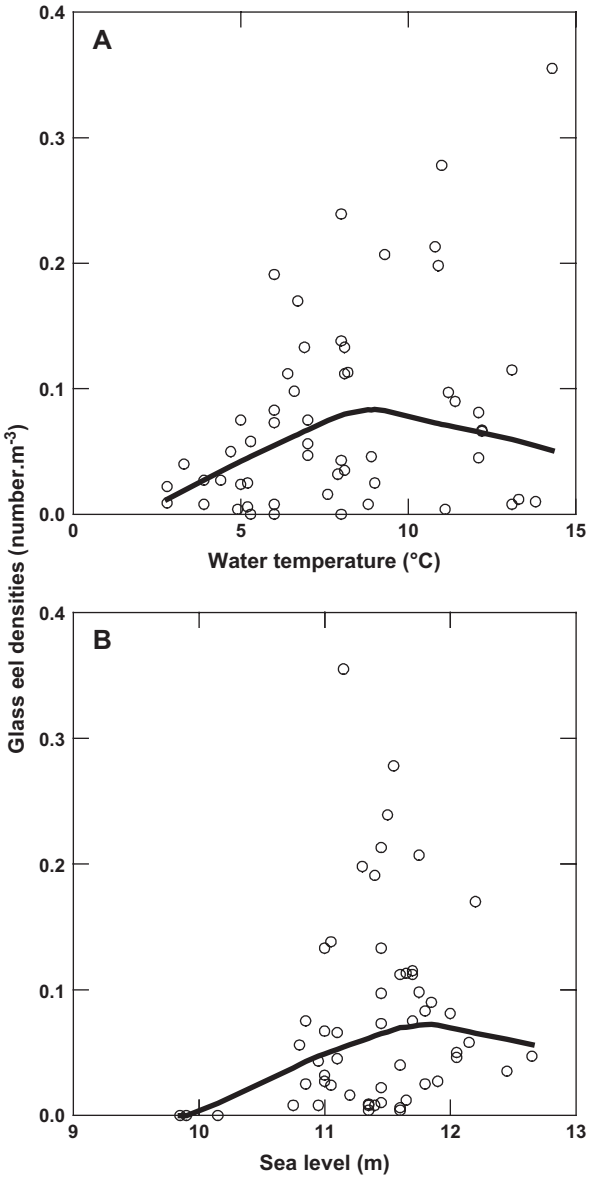

Fig. 7. Scatter plot of glass eel densities (number per m^3) caught upstream of the dam versus water temperature (A) and sea level (B). Smoothing was performed using the LOWESS non-parametric method (solid line) with tension $f = 0.8$.

were low at temperatures below 6 °C and/or a sea level below 11 m and densities were highest at temperatures between 8 and 12 °C and for sea levels between 11 and 12 m. These environmental conditions constitute the main windows of the recruitment period in the regulated Couesnon estuary.

4. Discussion

The densities of glass eels migrating upstream from the dam on the Couesnon estuary using the tidal currents were on average 0.15 fish m^{-3} between January and April 2004 and on average 0.09 fish m^{-3} between February and April 2005. These densities were two to three times lower than the densities on French Atlantic estuaries such as the Vilaine estuary (southern Brittany with a high estuarine dam) and the Loire estuary in the same winters, where the densities were measured during the same months and seasons using professional catches (Affaires Maritimes, Tableau de Bord Anguille du Bassin Loire and Professional Fishermen, pers. comm.). This difference is certainly the result of the catchment location in relation to the Gulf Stream, which is the principal vector for eel recruitment in European coastal areas (Tesch, 2003). Therefore, as with the Gulf Stream in the sea for leptocephali, the tidal current has to be considered as an abiotic vector for glass eels in estuaries.

When glass eels arrive in estuaries, the majority are in the VA glass eel stage. In estuaries, they become pigmented and the VB glass eel stage dominates (De Casamajor et al., 2003; Lefebvre et al., 2003; Briand et al., 2005b), being about 70% in the Couesnon estuary. The mean individual size of glass eels caught in the Couesnon estuary (69 mm and 0.29 g) is similar to the size estimated in other French Atlantic estuaries (Desaunay and Guerault, 1997; Lambert et al., 2003) and elsewhere in Europe (Dekker et al., 1998).

Glass eels migrating upstream showed a large seasonal variability in densities. During the 2004 and 2005 winter seasons, several peaks in glass eel densities were detected, at the end of January 2004 and in mid-March 2004 and 2005. The observation of several migration peaks is common in many estuaries and depends on two major factors, the reproductive period and the water temperature. In the Sargasso Sea, leptocephalus larvae about 5 mm long can be caught throughout the year, which suggests a long reproductive period (Boetius and Harding, 1985). However, the reproductive period is highest in spring (Mc Cleave, 1993), which could explain the winter peaks of glass eel recruitment on the Atlantic European coast. Moreover, Boetius and Boetius (1989) suggested that the transoceanic eel migration could be in successive recruitment waves, a hypothesis that has been confirmed by several studies on glass eel recruitment dynamics, on the Mediterranean coast (Ciccotti et al., 1995; Lefebvre et al., 2003) and on the Atlantic coast (Cantrelle, 1984). The two migration peaks in winter in the Couesnon estuary could be explained by the strong decrease in water temperature between these two periods. In fact, the glass eel becomes inactive when the water temperatures decrease to below 4−6 °C (Deelder, 1958; Elie and Rochard, 1994), the typical temperature of the Couesnon water in February. From April, when water temperatures were more than 10−12 °C, glass eels start to actively migrate (Gascuel, 1986; White and Knights, 1997). These high temperatures were only noted from April onwards in the Couesnon estuary.

Consistently higher captures occur at night than in the daytime (Elie and Rochard, 1994; Bardonnet et al., 2003). Thus, in addition to the tide, light plays a role in glass eel estuarine migration. De Casamajor et al. (1999) suggested that it is especially the vertical distribution of the glass eels in the water column that is modified by the light intensity. Glass eels were more abundant close to the bottom when the light intensity was strong. However, we found no relationship with light intensity, doubtless due to a high turbidity of the Couesnon estuarine water (mean more than 150 NTU). In fact, when the turbidity was greater than 100−150 NTU, Bardonnet et al. (2005) showed that light intensity has no influence on glass eel migration. The suspended solids' concentration can reach 1000 mg l^{-1}as a result of strong tidal scouring.

The quantity of glass eels that move through the dam openings depends on the quantity of glass eels that arrive at the dam. Not all glass eels migrated upstream because the dam was not totally permeable for this ecophase. Although the largest numbers of glass eels arrived downstream of the dam between the beginning and the middle of the flood tide, they migrated through the Couesnon estuarine dam openings preferentially from the middle of the flood to the beginning of ebb tide. The temporal shift in the recruitment pattern of eel is an important adverse effect of man-made barriers. In fact, dams and other physical barriers have two main impacts on the upstream migration of young eel. They either entirely stop the upstream migration because the dam is impassable or, as is most often the case, only allow a portion of the migrants to pass (because of mitigation measures taken such as the provision of an opening or of a fish pass). There is a third impact, that of migration delay, which as was found in the present study can be significant for glass eels. So, glass eels that migrate upstream of a dam take more time than glass eels that migrate without a dam for the same migration distance. Estuarine dam permeability is fundamental in the control of the glass eel population dynamics, because glass eel natural mortality is (1) intrinsically high, (2) density-dependent and (3) specifically high during the spring for glass eels blocked downstream of estuarine dams (Jessop, 2000; Briand et al., 2003). So, the management of estuarine dams is very important and fundamental for conserving the inland waters' part of the European eel population (see for example Briand et al., 2005a).

Selective transport by the tide is a major behavioural mechanism for the migration of many species of young and adult fish, including eels (Gascuel, 1986). According to the STST behavior, fish show a semi-diurnal vertical migration in phase with the tidal cycle. These fish, and especially glass eels, execute the upstream migrations in the water column during the flood and remain on the bottom substrate during the ebb, when the tide is in the opposite direction to their migration. This phenomenon of vertical migration could be perhaps due to an internal clock (Mc Cleave and Wippelhauser, 1987).

However, the temporal variation is slightly different at the Couesnon dam because it is based on the water level differences between upstream and downstream of the dam. Indeed, the glass eel densities were highest when the difference in water level was greatest, at the end of the flood (second half of the flood and first third of the ebb). When the differences in water level were low, the densities of glass eels were also low. Thus, very few glass eel were captured starting in the second half of the ebb and none were caught when there was no difference in water levels, which lasted on average from 5 to 10 min. The glass eels were, therefore, transported passively past the dam by upstream water movements caused by the water level difference between the upstream and the downstream part of the dam. The upstream migration dynamics, therefore, depends on the tidal rhythms and heights, which provide access to the upstream area when sufficiently high. Wippelhauser and Mc Cleave (1988) suggest that water current inversion is an effective synchronizer of glass eel activity in zones subjected to the influence of the tide. Finally, glass eel could not swim upstream when the tidal gates of the Couesnon dam were open because (1) the majority of glass eels in estuaries are in the passive migration phase, especially in the downstream area (more than 90% of eels were in the VB–VIA1 stage in the Couesnon estuary), (2) during this passive migration phase, the glass eels could not swim actively upstream in the estuary, and (3) glass eels migrate upstream only using the tidal currents via selective tidal stream transport (Gascuel, 1986; Beaulaton and Castelnaud, 2005).

The spatial and temporal dynamics of glass eel migration results generally from three different interacting factors. The first is inherent to the overall composition of the glass eel cohort that depends on the developmental stage as well as on the physiological state of individual fish (Desaunay and Guerault, 1997). The second factor is the estuarine abiotic conditions that affect the patterns of population dynamics (Jellyman and Lambert, 2003), and also the individual response to environmental stimuli (Edeline et al., 2004). The third and certainly the strongest factor is extrinsic and is represented by the hydrological dynamics of the water masses in the estuary, that drives the upstream transport of glass eels when they are in their passive phase and facilitates or opposes their active swimming performances when in the colonization stage (Gascuel, 1986; Mc Cleave and Wippelhauser, 1987). However, the spatial and temporal dynamics of glass eel migration changes in relation to abnormalities in the migration progress such as ecological disturbances caused by dams. In this study, the ANN model showed that two environmental variables had the highest significant effects on the densities of glass eels colonizing the upstream areas of the Couesnon estuary: sea level and water temperature. Other variables such as sea water salinity, water turbidity, water clarity and lunar phase contributed little to the models. Discharge is an important factor that could explain glass eel migration into European (Elie and Rochard, 1994), American (Jessop, 2003) and Australasian (Jellyman and Lambert, 2003) estuaries. But estuarine dams stop partially or totally the river current during the flood and ebb tide, especially in the Couesnon where the freshwater flow is very low and totally stopped by the dam. Consequently river discharges were not used in our study. There is no upstream movement of glass eel on an outgoing or low tide in some estuaries (Gascuel, 1986; Beaulaton and Castelnaud, 2005). The presence of the dam essentially means that glass eels are never subjected to freshwater temperature until they pass through the apertures in the dam gates. Freshwater temperature is, therefore, irrelevant. Furthermore. we never observed a large difference (always less than 2 °C) in the temperature between the sea and the river. This difference is well below the 3–4 °C level which Mc Govern and Mc Carthy (1992) report as affecting glass eel migration.

There are three means of passing upstream-migrating eel over barriers: (1) glass eels could be captured downstream of the dam and could then be stocked upstream, (2) specific eel-passes could be installed and (3) the structure and/or management of its operation could be designed to maximise passage. The most common technique currently used to increase population density upstream of barriers is stocking (Robak, 1994; Moriarty and Dekker, 1997; Roncarati et al., 1997), but this technique is, however, only efficient for elvers and young yellow eels and not for glass eels. It is also expensive in terms of manpower, equipment and time. Furthermore, the collection of glass eels does adversely affect the young of many marine fish species that are inadvertently gathered (Sobrino et al., 2005). Eel-passes are essentially ineffective for glass eels because the majority of glass eels in estuaries are in a passive migration phase. In this early phase, glass eels do not crawl out of the water, so are incapable of ‘‘climbing’’ over obstructions as they do later as elver and juvenile yellow eels (Legault, 1988; Legault, 1992). Effective structure design and targeted operational procedures are invariably the least expensive and most efficient means of allowing eel passage at instream barriers (Legault, 1990). As we have shown, this approach has been used with some success at the Couesnon dam. To increase passage efficiency at managed structures, the timing of the migration and the factors that affect it have to be known. This information is best obtained by in depth field studies coupled to models such as the ANN analysis used in the present study. Because of the substantial decline in European eel recruitment improving passage at the multitude of estuarine barriers that exist through most of Europe is urgently required. As the design of these barriers is variable and local condition differs, site specific investigations and solutions will be required.

Acknowledgments

This study was funded by the Syndicat Mixte Baie du Mont-Saint-Michel and the Mission Mont-Saint-Michel (DDE Manche). The help of many colleagues was also indispensable in the fieldwork, thanks to them. We thank A. Baisez (Tableau de Bord Anguille du Bassin Loire, Logrami), C. Briand (Institut d’Aménagement de la Vilaine), G. Berrée (DDE Manche) and J. Boubee (NIWA) for many helpful suggestions, and the three anonymous referees for critical and valuable suggestions on this manuscript.

References

Baisez, A., Laffaille, P., 2005. Un outil d'aide à la gestion de l'anguille: le tableau de bord anguille du bassin Loire. Bulletin Français de la Pêche et de la Pisciculture 378/379, 115−130.

Bardonnet, A., Dasse, S., Parade, M., Heland, M., 2003. Influence de l'alternance jour/nuit sur les déplacements de civelles en flumarium. Bulletin Français de la Pêche et de la Pisciculture 368, 9−20.

Bardonnet, A., Bolliet, V., Belon, V., 2005. Recruitment abundance estimation: role of glass eel (*Anguilla anguilla* L.) response to light. Journal of Experimental Marine Biology and Ecology 321, 181−190.

Beaulaton, L., Castelnaud, G., 2005. The efficiency of selective tidal stream transport in glass eel entering the Gironde (France). Bulletin Français de la Pêche et de la Pisciculture 378−379, 5−21.

Boetius, I., Boetius, J., 1989. Ascending elvers, *Anguilla anguilla*, from five European localities. Analyses of pigmentation stages, condition, chemical composition and energy reserves. Dana 7, 1−12.

Boetius, J., Harding, E.F., 1985. A re-examination of Johannes Schmidt's Atlantic eel investigations. Dana 4, 129−162.

Briand, C., Fatin, D., Fontenelle, G., Feunteun, E., 2003. Estuarine and fluvial recruitment of the European glass eel, *Anguilla anguilla*, in an exploited Atlantic estuary. Fisheries Management and Ecology 10, 377−384.

Briand, C., Fatin, D., Fontenelle, G., Feunteun, E., 2005a. Effect of re-opening of a migratory pathway for eel (*Anguilla anguilla*, L.) at a watershed scale. Bulletin Français de la Pêche et de la Pisciculture 378−379, 67−86.

Briand, C., Fatin, D., Ciccotti, E., Lambert, P., 2005b. A stage-structured model to predict the effect of temperature and salinity on glass eel *Anguilla anguilla* pigmentation development. Journal of Fish Biology 67, 993−1009.

Cantrelle, I., 1984. Les populations de civelles d'*Anguilla anguilla* L. en migration dans l'estuaire de la Gironde. Vie Milieu 34, 109−116.

Ciccotti, E., Ricci, T., Scardi, M., Fresi, E., Cataudella, S., 1995. Intraseasonal characterization of glass eel migration in the River Tiber: space and time dynamics. Journal of Fish Biology 47, 248−255.

Daverat, F., Limburg, K.E., Thibault, I., Shiao, J.-C., Dodson, J.J., Caron, F., Tzeng, W.-N., Iizuka, Y., Wickström, H., 2006. Phenotypic plasticity of habitat use by three temperate eel species, *Anguilla anguilla*, *A. japonica* and *A. rostrata*. Marine Ecology Progress Series 308, 231−241.

De Casamajor, M.N., Bru, N., Prouzet, P., 1999. Influence de la luminosité nocturne et de la turbidité sur le comportement vertical de migration de la civelle d'anguille (*Anguilla anguilla* L.) dans l'estuaire de l'Adour. Bulletin Français de la Pêche et de la Pisciculture 355, 327−347.

De Casamajor, M.N., Lecomte-Finiger, R., Prouzet, P., 2003. Caractéristiques biologiques des civelles (*Anguilla anguilla*) lors de la transition en estuaire. Bulletin Français de la Pêche et de la Pisciculture 368, 109−124.

Deelder, C.L., 1958. On the behaviour of elvers (*Anguilla vulgaris* Turt.) migrating from the sea into freshwater. Journal du Conseil Permanent International pour l'Exploration de la Mer 24, 135−146.

Dekker, W., 2003. Did lack of spawners cause the collapse of the European eel, *Anguilla anguilla*? Fisheries Management and Ecology 10, 365−376.

Dekker, W., Van Os, B., Van Willigen, J., 1998. Minimal and maximal size of eel. Bulletin Français de la Pêche et de la Pisciculture 349, 195−197.

Desaunay, Y., Guerault, D., 1997. Seasonal and long-term changes in biometrics of eel larvae: a possible relationship between recruitment variation and North Atlantic ecosystem productivity. Journal of Fish Biology 51, 317−339.

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

Edeline, E., Dufour, S., Briand, C., Fatin, D., Elie, P., 2004. Thyroidal status is related to migratory behaviour in glass eels of *Anguilla anguilla*. Marine Ecology Progress Series 282, 261−270.

Edeline, E., Dufour, S., Elie, P., 2005. Role of glass eel salinity preference in the control of habitat selection and growth plasticity in *Anguilla anguilla*. Marine Ecology Progress Series 304, 191−199.

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.

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

Elie, P., Rochard, E., 1994. Migration des civelles d'anguilles (*Anguilla anguilla* L.) dans les estuaires, modalités du phénomène et caractéristiques des individus. Bulletin Français de la Pêche et de la Pisciculture 335, 81−98.

Feunteun, E., 2002. Restoration and management of the European eel: an impossible bargain? Ecological Engineering 18, 575−591.

Gascuel, D., 1986. Flow-carried and active swimming migration of the glass eel (*Anguilla anguilla*) in the tidal area of a small estuary on the French Atlantic coast. Helgoländer Meeresuntersuchungen 40, 321−326.

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

ICES, 1999. Report of the ICES Advisory Committee on Fisheries Management, 1998. International Council for the Exploration of the Sea, Copenhagen. ICES Cooperative Research Report 229, 819−828.

Jellyman, D.J., Lambert, P.W., 2003. Factors affecting recruitment of glass eels into Grey River, New Zealand. Journal of Fish Biology 63, 1067−1079.

Jessop, B.M., 2000. Estimates of population size and instream mortality rate of American eel elvers in a Nova Scotia River. Transaction of the American Fisheries Society 129, 514−526.

Jessop, B.M., 2003. Annual variability in the effects of mater temperature, discharge, and tidal stage on the migration of American eel elvers from estuary to river. American Fisheries Society Symposium 33, 3−16.

Knights, B., White, E., 1998. Enhancing immigration and recruitment of eels: the use of passes and associated trapping system. Fisheries Management and Ecology 5, 459−471.

Kirk, R.S., 2003. The impact of *Anguillicola crassus* on European eels. Fisheries Management and Ecology 10, 385−394.

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

Laffaille, P., Thieulle, L., Feunteun, E., Lefeuvre, J.-C., 2000b. Composition of fish community in small anthropic estuary (The Couesnon, France). Bulletin Français de la Pêche et de la Pisciculture 357/358, 191−208.

Lambert, P., Sbaihi, M., Rochard, E., Marchelidon, J., Dufour, S., Elie, P., 2003. Variabilités morphologiques et du taux d'hormone de croissance des civelles d'anguilles européennes (*Anguilla anguilla*) dans l'estuaire de la Gironde au cours de la saison 1997−1998. Bulletin Français de la Pêche et de la Pisciculture 368, 69−84.

Lefebvre, F., Sergent, E., Acou, A., Lecomte-Finiger, R., Crivelli, A.J., 2003. Recrutement des civelles (*Anguilla anguilla*) sur la côte méditerranéenne Française: analyse comparée des caractéristiques biométriques et pigmentaires des saisons 1974−75 et 2000−01. Bulletin Français de la Pêche et de la Pisciculture 368, 85−96.

Legault, A., 1988. Le franchissement des barrages par l'escalade de l'anguille: étude en Sèvre Niortaise. Bulletin Français de la Pêche et de la Pisciculture 308, 1−10.

Legault, A., 1990. Gestion des barrages estuariens et migration d'anguilles. Internationale Revue Gesamten Hydrobiologie 75, 819−825.

Legault, A., 1992. Etude de quelques facteurs de sélectivité de passes à anguilles. Bulletin Français de la Pêche et de la Pisciculture 325, 83−91.

Lek, S., Guégan, J.F., 1999. Artificial neural networks as a tool in ecological modelling, an introduction. Ecological Modeling 120, 65−73.

Mc Cleave, J.D., 1993. Physical and behavioural controls on the oceanic distribution and migration of leptocephali. Journal of Fish Biology 43, 243−273.

Mc Cleave, J.D., Wippelhauser, G.S., 1987. Behavioral aspects of selective tidal stream transport in juvenile American eels. American Fisheries Society Symposium 1, 138−150.

Mc Govern, P., Mc Carthy, T.K., 1992. Elvers migration in the River Corrib system, western Ireland. Irish Fisheries Investigations Series A 36, 25−32.

Moriarty, C., Dekker, W. (Eds.), 1997. Management of European eel Fisheries. Irish Fishery Bulletin 15, 1−110.

Robak, S., 1994. Stocking of young eels and spring downstream migration of small eel *Anguilla anguilla* ($W < 300$ g) in the River Sapina Basin (Great Mazurian Lake district, Poland). Bulletin of the Sea Fisheries Institute 132, 3−11.

Roncarati, A., Melotti, P., Mordenti, O., Gennari, L., 1997. Influence of stocking density of European eel (*Anguilla anguilla*, L.) elvers on sex differentiation and zootechnical performances. Journal of Applied Ichthyology 13, 131−136.

Rosell, R., Evans, D., Allen, M., 2005. The eel fishery in Lough Neagh, Northern Ireland − an example of sustainable management? Fisheries Management and Ecology 12, 377−385.

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

Russell, I.C., Potter, E.C.E., 2003. Implications of the precautionary approach for the management of the European eel, *Anguilla anguilla*. Fisheries Management and Ecology 10, 395−401.

Sobrino, I., Baldo, F., Garcia-Gonzalez, D., Cuesta, J.A., Silva-Garcia, A., Fernandez-Delgado, C., Arias, A.M., Rodriguez, A., Drake, P., 2005. The effect of estuarine fisheries on juvenile fish observed within the Guadalquivir estuary (SW Spain). Fisheries Research 76, 229−242.

Tesch, F.W., 2003. The Eel. In: Thorpe, J.E. (Ed.), third ed. Blackwell Publishing, London, p. 336.

Trexler, J.C., Travis, J., 1993. Nontraditional regression analyses. Ecology 74, 1629−1637.

White, E.M., Knights, B., 1997. Environmental factors affecting migration of the European eel in the Rivers Severn and Avon, England. Journal of Fish Biology 50, 1104−1116.

Wippelhauser, G.S., Mc Cleave, J.D., 1988. Rhythmic activity of migrating juvenile American eels *Anguilla rostrata*. Journal of the Marine Biology Association of the UK 68, 81−91.