To link to this article: DOI:10.1111/j.1600-0633.2008.00295.x
URL: http://dx.doi.org/10.1111/j.1600-0633.2008.00295.x

To cite this version: Acou, Anthony and Laffaille, Pascal and Legault, Antoine *Migration pattern of silver eel (Anguilla anguilla, L.) in an obstructed river system.* (2008) Ecology of Freshwater Fish, Vol. 17 (n° 3). pp. 432-442. ISSN 1600-0633

Migration pattern of silver eel (*Anguilla anguilla*, L.) in an obstructed river system

Acou A, Laffaille P, Legault A, Feunteun E. Migration pattern of silver eel (*Anguilla anguilla*, L.) in an obstructed river system.

A. Acou[1], P. Laffaille[1], A. Legault[2], E. Feunteun[3]

[1]Université de Rennes 1, Equipe Recherche et Technologie 52 «Biodiversité Fonctionnelle et Gestion du Territoire» Rennes, France, [2]Fish Pass, Bureau Expert Gestion Piscicole, Laillé, France, [3]Muséum National d'Histoire Naturelle, Laboratoire Maritime de Dinard, Dinard, France

Abstract – The downstream migration of European silver eels in the River Frémur was examined to determine the potential effects of the numerous migration barriers that exist on waterways in western France. The Frémur has a 14 m high dam which creates a 3×10^6 m^3 water supply reservoir, 6 km from tidal limit. Based on 8-year records (1996–2004) of migrant silver eels captured in a Wolf trap located about 1 km below the dam, the influence of this dam on the migration was examined. These records indicate that 91% of silver eels were captured when the dam was overtopped (i.e. when the water reservoir was full). The timings of the overflow periods varied greatly between years mainly because they are function of the duration of the filling period which in turn is dependent on the level of summer water abstraction and annual hydrological conditions. Consequently, migration periods occurred at variable dates (between November and April) which is late in comparison with nonobstructed European river systems (generally between August and December). During overflow periods the migration of silver eels increased markedly during rain events (increasing river flow). This indicates that flow flushes, are essential so that settled silver eels can orientate themselves and pass over the dam. The hypothesis of a 'dam effect' that could stop temporarily or permanently some of silver eels in the reservoir is discussed. Finally, the influence of the migration delays on the condition of silver eels is considered.

Key words: *Anguilla anguilla*; downstream migration; dam; water reservoir; environmental factors

A. Acou, Université de Rennes 1, Equipe de Recherche Technologique 52, Biodiversité Fonctionnelle et Gestion du Territoire, Bâtiment 25, Campus de Beaulieu, 35042 Rennes, France; e-mail: anthony.acou@univ-rennes1.fr

Introduction

After a variable growth period (from 3 to more than 20 years) during which they become subadults (silver eels), European eels *Anguilla anguilla* (L) leave continental habitats and join the sea. These silver eels then make a journey of several thousand kilometres to reach the Sargasso Sea spawning zone and reproduce (Schmidt 1922; Tesch 2003). The beginning of this migration depends on both endogenous and exogenous factors. Indeed, eels migrate after they metamorphose into silver eels (Acou et al. 2005; Durif et al. 2005; van Ginneken et al. 2007). The silvering process involves a series of morphological and physiological transformations that mark the transition between a sedentary growth phase (yellow eel) and a catadromous migration phase (silver eel) which prepares them for the deep sea migration. Because the silvering process preadapts eels to the marine conditions while they are still in freshwater, it generates a physiological instability (osmotic imbalance notably) that predisposes fishes to migrate. It is at the end of the silvering process that usually occurs in late summer (van Ginneken et al. 2007) that silver eels wait for favourable environmental windows to begin their seaward migration.

In natural environment and for temperate species including Atlantic species (*A. anguilla* and *A. rostrata*) and those from New Zealand (*A. australis* and *A. dieffenbachii*), migrations generally take place in autumn when water temperature decreases (Todd 1981; Haraldstad et al. 1985; Hvidsten 1985; Vøllestad et al.

doi: 10.1111/j.1600-0633.2008.00295.x

1986; Haro 1991; Boubée et al. 2001; Cullen & McCarthy 2003). The moon periodicity may also be an important factor for the migration because eels tend to be more active during the second half of the lunar cycle (Frost 1950; Todd 1981; Deelder 1984; Cullen & McCarthy 2003). Furthermore, rain, flow increases and the passage of depressions could also influence the migration behaviour of silver eels as they are often caught during stormy nights (Todd 1981; Vøllestad et al. 1986; Boubée et al. 2001). The onset of the migration thus takes place during environmental windows set by seasonal (e.g. temperature), monthly (e.g. moon) and daily (e.g. atmospheric pressure, pluviometry and water flow) patterns.

Anthropogenic factors notably the construction of dams can markedly perturb the seaward migration of silver eels (Travade & Larinier 1992; Boubée et al. 2001). Passage through turbines and discharge facilities (e.g. outflow pipe) can often induce high or even total mortality depending upon characteristics of the plant and its mode of operation (Berg 1986; Legault et al. 2003; Gosset et al. 2005; Watene & Boubée 2005). Numerous telemetry studies have shown that the behaviour of silver eels in front of the dam varies (e.g. temporary and/or complete end of the migration, return upstream, etc.); depending on the individual, the physical characteristics of the obstacles and the local environmental conditions (Haro et al. 2000; Behrmann-Godel & Eckmann 2003; Durif et al. 2003). However, few of these studies have considered the effects such delay on the migratory dynamics of silver eels. With the decline of the European eel stocks (Moriarty & Dekker 1997), a better understanding of the eel migratory dynamics is required both at local and continental levels so that means of ensuring maximum escape of silver eel from each catchment can be devised (Feunteun 2002; Baisez & Laffaille 2005; Laffaille et al. 2006; Acou et al. in press).

In the present study, we examine the migration of silver eels in the Frémur, an obstructed river representative of numerous western coastal hydrosystems of France (see Feunteun et al. 2000 for a detailed description). A 14 m high dam which creates a 3×10^6 m^3 water supply reservoir is present on the stream. A Wolf trap located about 1 km downstream provided the opportunity to analyse the influence of this dam on the migration. Previous studies indicated that silver eel migrations occurred during periods of reservoir overflow (Acou et al. 2000; Feunteun et al. 2000). Temporal pattern of the silver eels captures was analysed over an 8-year period (from 1996 to 2004) and eel numbers related to: (i) spilling flows (ii) lunar phases and (iii) environmental factors (temperature, atmospheric pressure, rainfall and water discharge).

Material and methods

Study site

The Frémur is a small river of northern Brittany (France) which opens into the English Channel next to Saint Malo (longitude 2°04'W, latitude 48°32'N). The catchments area is about 60 km^2 and the overall length of the river and tributaries is 45 km, with 17 km for the mainstem. The channel slope varies between 0.1% and 2% with an average of 0.6%. Despite its small size, the Frémur has a wide range of habitats varying from high velocity trout zones to lentic bream zones including man-made ponds and reservoirs, wetlands, etc. The total water surface is 75 ha including 5 ha of running waters (streams) and 70 ha of still waters.

A total of six dams and weirs are present on the catchment. Three of them were complete upstream fish migration barriers until they were equipped with eel passes to restore upstream migration (Feunteun et al. 1998; Fig. 1). The Bois Joli Dam (6 km from the estuary) is the most important migration barrier. It has been equipped with an eel lift to restore upstream migration, but no equipment has been provided for downstream migration. This 14 m high dam creates a 3×10^6 m^3 water supply reservoir to provide the county with drinking water. The reservoir stores water in winter to provide this important tourist region with water from March to November. In Brittany, the presence of such dams is rather common as 27 water reservoirs of more than 0.5×10^6 m^3 in river catchments have been listed (see the web site http://eaubretagne.fr/article/les-retenues-artificielles, 12 February 2008). The Bois Joli overflow crest is 28.20 m NGF (Niveau Général de la France; baseline mean sea level for France). A minimum flow of 0.04 m^3·s^{-1} is provided below the dam with a compensation flow pipe. This is the only flow available when water levels in the reservoir are below 28.20 m NGF. A survey of the silver eels migration through this pipe, carried out between October 1998 and January 1999, showed that only a small proportion of silver eels (about 12% on average) used this route to emigrate. The compensation flow pipe is used, not only at the beginning of the downstream run when this is the only passage available but also later when water overflowing the weir allows eels to pass over the weir crest (Legault et al. 2003). Number of silver eels caught in the pipe increased with increasing natural water discharge (Legault et al. 2003) suggesting that the proportion of silver eels using this route was maximum (about 12% on average) during overflow period. Furthermore, eels passing through the pipe are liable to abrasion injury and death (Legault et al. 2003). Therefore, the principal and only safe route

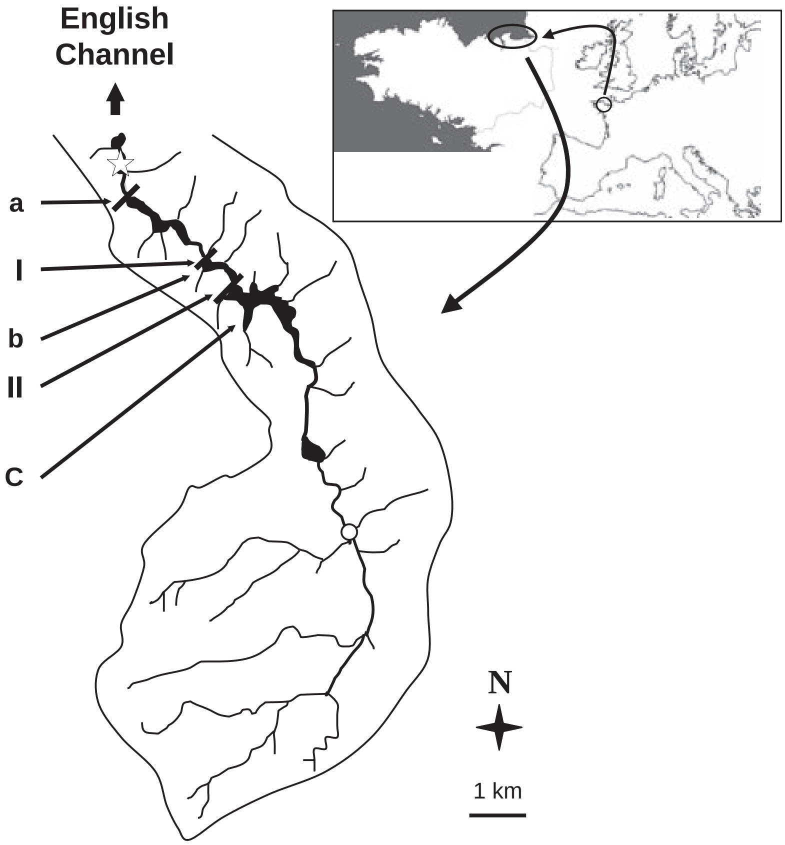

Fig. 1. Location and characteristics of the Frémur's catchment (longitude 2°04'W, latitude 48°32'N). Bars indicate the locations of major dams. (a) Pont Avet reservoir (2 km from the river mouth); (b) Pont es Omnes pond (4.5 km from the sea); (c) Bois Joli reservoir (6 km from the sea); I, silver eel trap; II, Bois Joli dam. The star and circle represent the tidal limit and the location of the gauging weir station respectively.

available for downstream migrant is over the weir when the reservoir is full (i.e. water level ≥28.20 m NGF).

Sampling

A Wolf trap was installed on the dam of 'Pont es Omnes' weir (4.5 km from the estuary Fig. 1) to capture descending eel over 200 mm under practically every flow conditions. Monitoring was conducted between September 1996 and August 2004 (i.e. over eight downstream migration seasons), with count of descending eel made from 1 September to 31 August each season. Over this period, the trap was inspected approximately once every 2 days but every day during migration peaks. Each fish collected was anaesthetised with Benzocaine at a concentration of 0.15 $g \cdot l^{-1}$ and measured [total length (TL) to the nearest mm]. Eels were allowed to recover in cool, well-oxygenated water for about 15 min before being returned to the stream. Silver eels were identified by three criteria: colour of the back and belly, presence of a well-defined lateral line (Acou et al. 2005, 2006) as well as ocular index (OI ≥6.5, Pankhurst's 1982). OI is the relation between TL and the mean size of the two eyes, calculated as: $OI = 25\pi/8\ TL \times [(A + B)^2_R + (A + B)^2_L]$ where TL is the total length, A and B the horizontal and vertical eye diameters and R and L are right and left eyes. If only two of the criteria (most often the lateral line and the OI value) were met, the eel was designated as yellow/silver eel. If only one criteria (generally the OI value) or none was met, the eel was recorded as yellow (Feunteun et al. 2000). Between September 1996 and June 1998, a total of 19 escapement tests were made by releasing eel batches (19–57 fishes) at the top of Pont es Omnes trap (Feunteun et al. 2000). The escapements were close to 0% except during a very short period (5 days) when the river flow exceeded 1500 $l \cdot s^{-1}$ at which water overflowed the collecting gutter and some eels could escape. During this high overflow period, escapement was on average 37% (varied from 9% to 67%). Based on assumed losses at critically river flows, corrections of daily catches with this average escapement rate were made for each day of the 1996–1998 period (5 days) and remaining period (i.e. 13 days in 1998–2004) when river flow exceeded 1500 $l \cdot s^{-1}$. The use of an average escapement rate may lead to underestimation of daily catches of migrant silver eels. However, the method used in this study was based on the percentage of maximum daily catch (see Data analysis and statistical treatments for more details) that limit the influence of this potential bias on our analysis.

Environmental parameters

To define the overflow periods, water level of the Bois Joli reservoir was measured every 2 days on a limnimetric board situated at the dam. Daily mean water discharge (in $m^3 \cdot s^{-1}$) was calculated from hourly flow records obtained at a gauging weir (Fig. 1). Daily river temperature (°C) was recorded with a data logger set at 1 m depth near the trap. Daily mean atmospheric pressure (in hPa) and rainfall (in $mm \cdot day^{-1}$) were obtained from a 'Meteo France' station located close (about 2 km) to the sampling area. Lunar phases were obtained using a freeware available on the 'Institut de Mécanique Céleste et de Calcul des Ephémérides' website (http://www.imcce.fr, 12 February 2008).

Data analysis and statistical treatments

Throughout the sampling period, small catches were occasionally made outside of the main migration seasons. To avoid distorting the analyses by including such outliers, the silver eel migration period was defined in a standard way as the period between the first day of overflow at the Bois Joli reservoir (i.e. water level ≥28.20 m NGF), to day of the last nonnull catch that was followed by three successive zero catches. Any other mid-season zero catches were retained in the analyses. These migration periods varied between 18 and 30 days and averaged 23.3 ± (SD) 5.1 days. For each migration period, daily catches were expressed as a percentage of the maximum daily catch obtained (MDCO). MDCO each season varied between 82 and 200 individuals and averaged 162 ± 96 silver eels. This method allowed comparison of temporal pattern between migration seasons despite an important interseasonal variability (Acou 2006). To ascertain the effect of environmental factors on catches the difference in river temperature, atmospheric pressure, water discharge and rainfall was calculated between consecutive days. These differences were than ranked as recommended by Escofier & Pages (1988) with three classes of daily variability used for the environmental factors: 1 = decreasing, 2 = stable and 3 = increasing (Table 1). The lunar month was similarly divided into eight periods which include the four main lunar phases and their associated transition phases (Table 1). Because distribution of the records was nonnormal associations between MDCO and the four environmental factors as well as lunar phases were examined using a Kruskal–Wallis non-parametric test. When significant, *post hoc* Tukey tests were then used to determine significant differences between data pairs (Sokal & Rohlf 1989). For each analysis, the level of statistical significance used was $P < 0.05$. Whisker-and-box plots were used to present the distribution of MDCO. Treatments were performed using the STATISTICA software (Release 5.5, StatSoft, Inc., 1993, Tulsa, Oklahoma, USA).

Table 1. Means of the environmental variables measured during the eight downstream migration periods studied. Description of the variability classes used and proportion of the total migration period in each variability class is also given. The total migration period was 186 days (eight seasons of about 23 days each).

Variables	Mean ± SD (minimum; maximum)	Variability class	Range of daily differences	Relative number of days (%)
River temperature (°C)	9.2 ± 2.	1	−2.009 to −0.212	26.9
	(4.7; 16.1)	2	−0.176 to 0.165	39.2
		3	0.187 to 3.042	33.9
Atmospheric pressure (hPa)	1013.8 ± 10.2	1	−15.900 to −5.000	21.0
	(987.2; 1033.5)	2	−4.700 to 4.400	53.8
		3	4.700 to 22.200	25.3
Rainfall ($mm \cdot day^{-1}$)	3.3 ± 5.1(0.0; 29.4)	1	−29.000 to −0.200	46.8
		2	0.000	17.2
		3	0.200 to 28.000	36.0
Water discharge ($m^3 \cdot s^{-1}$)	0.7 ± 0.7	1	−2.920 to −0.071	34.9
	(0.1; 5.8)	2	−0.067 to 0.000	29.6
		3	0.001 to 3.540	35.5
Lunar phases		NM		4.3
		Towards FQ		23.7
		FQ		2.2
		Towards FM		14.5
		FM		3.2
		Towards LQ		23.1
		LQ		3.8
		Towards NM		25.3

Variability class 1: decreasing, 2: stable, 3: increasing. NM, new moon; FQ, first quarter; FM, full moon; LQ, last quarter.

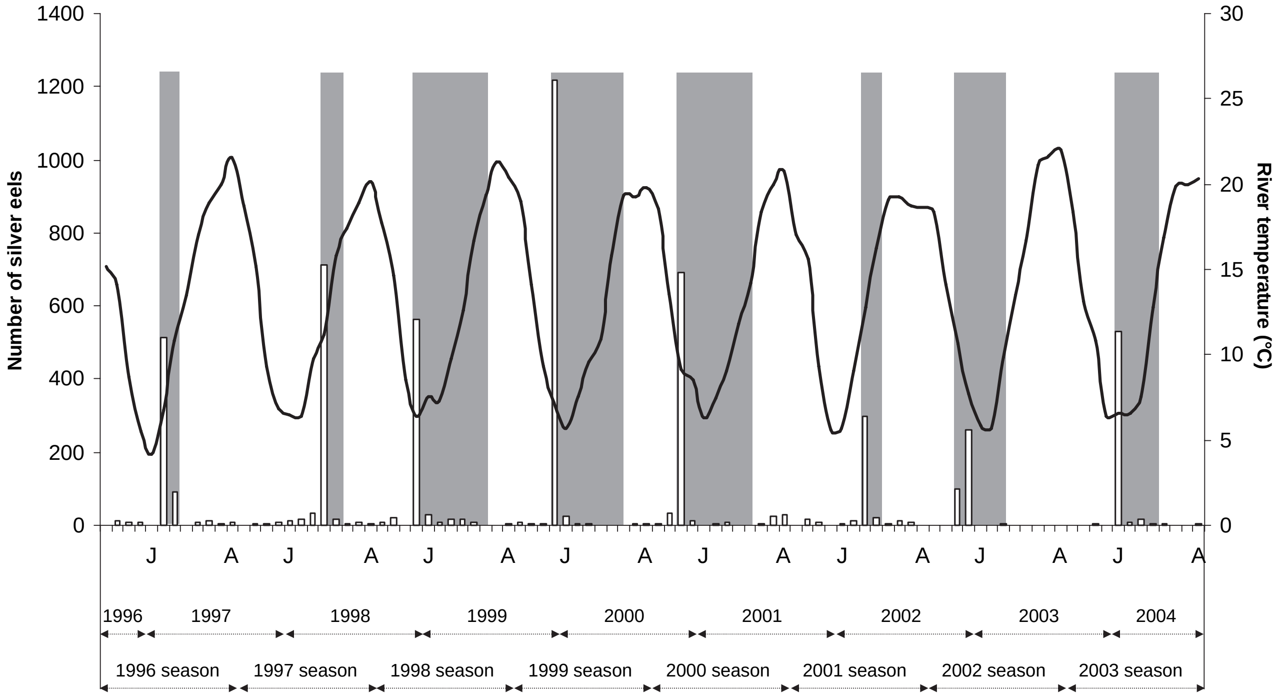

Fig. 2. Monthly silver eel emigration, monthly river temperatures and reservoir overflow period in the Frémur, September 1996 to August 2004. Bars are monthly catches at the Pont es Omnes Wolf trap, the line the average monthly river temperature and the shaded area the overflow period (water level ≥28.20 m NGF) at the Bois Joli Reservoir.

Results

A total of 6337 eels were caught in the downstream trap during the eight migrating seasons with the majority being silver eels (88.4%). The remaining eels were yellow (9.6%) and yellow/silver (2.0%) eels, so were excluded of the analysis.

Long-term periodic factor

During the study period, silver eels were captured every month of the year. However, 91% of silver eels captures were obtained during the overflow period (i.e. when the Bois Joli water level ≥28.20 m NGF; Fig. 2). The timing of the annual migration peaks varied from the end of autumn (i.e. November for the 2000 migration season) to the beginning of spring (i.e. April for the 1997 season) with most of migrations occurring in December (i.e. 1998, 1999 and 2004 season). During the nonoverflow periods, the majority (57%) of silver eel catches were made between August and December (Fig. 2). Silver eel catches were made over a temperature range of 4 to 23 °C, with about 76.5% of eels catches obtained when temperatures were between 6 and 10 °C (Fig. 3). However, monthly silver eel catches were only weakly correlated with mean monthly water temperature ($r^2 = 0.06$; $P < 0.05$).

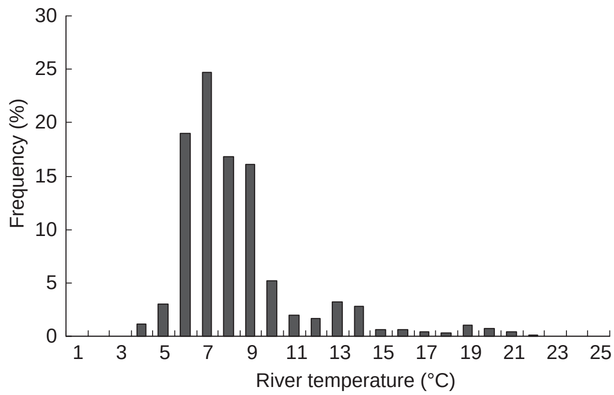

Fig. 3. Frequency distribution of migrant silver eel captured at different river temperatures from the Pont es Omnes Wolf trap, September 1996 to August 2004 (N = 5600 silver eels).

Effects of the environmental factors during the overflow period

During the eight overflow periods, highest MDCO were observed between 6 and 9 days after the beginning of the overflow (Fig. 4). Once spilling started, 2 weeks were sufficient to catch about 90% of the silver eels migrating. Consequently, any environmental effects of any consequences would have to affect the migration over this short 2 weeks period.

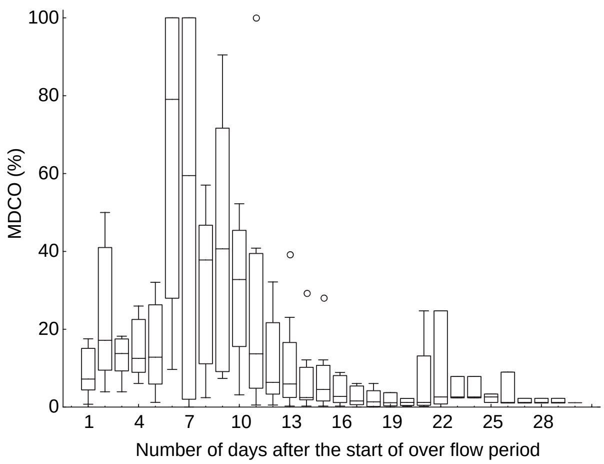

Fig. 4. Whisker-and-box plots showing median, 25th and 75th percentile and range of maximum daily catch obtained (MDCO) (%) according to the number of days after the start of overflow period observed at the Bois Joli Dam between September 1996 and August 2004. The outliers described in the text are indicated by open circles.

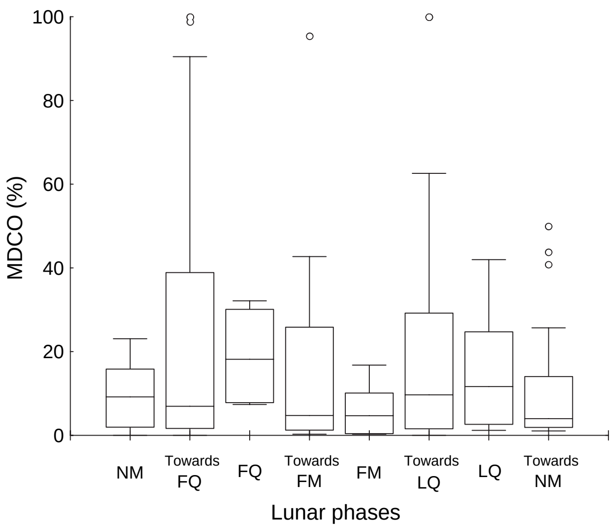

Fig. 5. Whisker-and-box plots showing median, 25th and 75th percentile and range of maximum daily catch obtained (MDCO) (%) and lunar phases during the Bois Joli Dam overflow periods. The outliers described in the text are indicated by open circles. NM, new moon; FQ, first quarter; FM, full moon; LQ, last quarter.

No significant difference in MDCO was identified when considering lunar phases (Kruskal–Wallis test, $P > 0.05$; Fig. 5). Except for river temperature, mean ranks of MDCO were significantly different among the three variability class for atmospheric pressure, rainfall and water discharge (Kruskal–Wallis tests, all $P < 0.05$). Observing the mean ranks by variability class and the whisker-and-box plots (Fig. 6), we can state that MDCO was higher during atmospheric depression and high river discharge and lower when pluviometry was stable.

Discussion

In the Frémur River, the seaward migration of silver eels is strongly affected by the water level of the Bois Joli reservoir. Indeed, nearly 90% of total migrant silver eels captured in the Pont es Omnes Wolf trap were obtained <2 weeks after the start of the overflow period, i.e. when the Bois Joli reservoir is full and the water level is above 28.20 m NGF. During the overflow period but also when the water reservoir is filling, only 12% of silver eels passed the Bois Joli Dam through the pipe that provides the minimum flow downstream of the dam (Legault et al. 2003). Consequently, during overflow periods, nearly 90% of the silver eels captured in the Pont es Omnes Wolf trap passed over the crest of the Bois Joli Dam and slid down the 14 m high dam. A PIT (Passive Integrated Transponder)-tagging survey realised between the pipe and the Pont es Omnes Wolf trap in 1998 showed that 80% of tagged silver eels reached quickly (3.5 days on average) the trap once spilling started (Legault et al. 2003), suggesting that the Pont es Omnes pond had little influence on silver eels migration dynamics during overflow period. However, when there was no overflow the majority of migrant silver eels captured in the Wolf trap were likely to be eels that had staged in the Pont es Omnes pond to await favourable environmental conditions to migrate.

The timing and duration of the overflow periods are highly variable because they depend on the duration of the filling period which in turn is dependent on the annual hydrological conditions and the level of summer water abstraction (Legault et al. 2003). Consequently, the timing of the silver eel seaward migration peaks are also variable and can occur as early as November (season 2000) and as late as April (season 1997), but mostly take place in December (seasons 1998, 1999 and 2002). These migrations are late in comparison with those described in the literature. Indeed, the seaward migration of the European eel generally takes place in autumn between August and December (Behrmann-Godel & Eckmann 2003; Tesch 2003; Chadwick et al. 2007). However, in nonobstructed systems the seaward migration peaks can begin in July and continue until spring, if climatic conditions for migration are favourable (Frost 1950; Deelder 1984; Hvidsten 1985; Lobon-Cervia & Carrascal 1992; Wickström et al. 1996). In Sweden, Holmgren et al. (1997) also mentioned that seaward migration in the Fardime träsk Lake may occur in autumn and spring. Similar observations were made by Chadwick et al. (2007) in a small Scottish River. However, these authors stipulated that the spring migration consisted of small eels (TL: 140–180 mm) and so were most likely sexually undifferentiated nomadic eels (as described by Feunteun et al. 2003), and not silver eels.

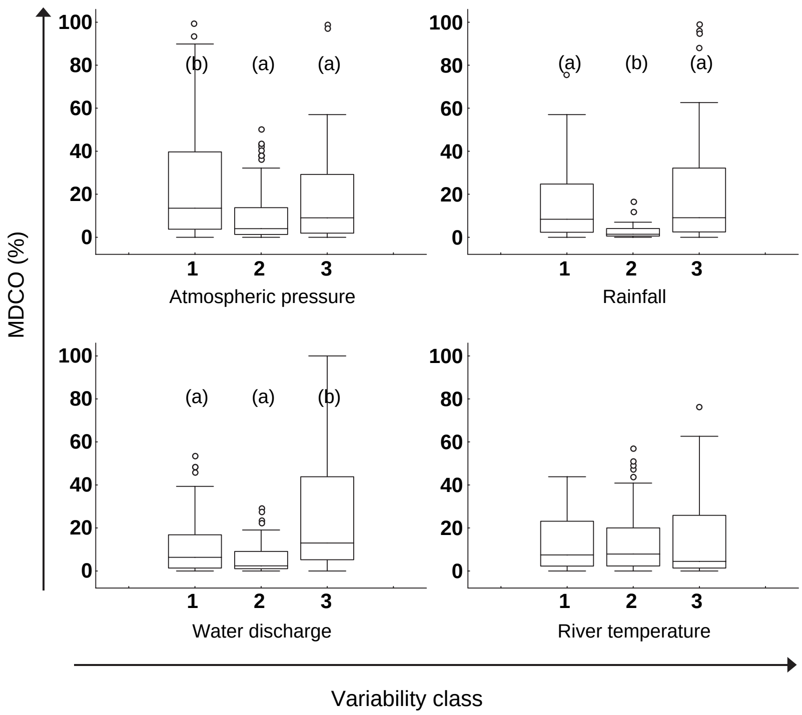

Fig. 6. Whisker-and-box plots showing median, 25th and 75th percentile and range of maximum daily catch obtained (MDCO) (%) according to the three variability class of atmospheric pressure, rainfall, water discharge and river temperature during Bois Joli Dam overflow periods. The outlier described in the text are indicated by open circles. Different letters in brackets denote variability class that were different ($P <$ 0.05) using Tukey's multiple comparisons tests after a significant Kruskal–Wallis test (Sokal & Rohlf 1989).

Consequences of a delay in the migration and the breeding success of these eels remain unknown. Numerous studies have demonstrated that altered migration condition in rivers caused by the construction of dams and reservoirs significantly impairs the migration success of others diadromous species. For instance, Congleton et al. (2002) monitored the physiological condition and energy use of juvenile salmonids as they migrated downstream through the Snake River and Columbia River dams and reservoirs (WA, USA). They found that body lipid and protein masses decreased significantly with increased travel time. Slower migration forces juvenile salmonids to use energy reserves beyond levels expected to occur under free-flowing river that provides swift migration rates. Moreover, increased energy expenditure decreases a fish ability to avoid predators (Ryan et al. 2003), increases its vulnerability to disease (Plumb et al. 2006), and can change its disposition to enter the marine environment (Zaugg et al. 1985). Budy et al. (2002) concluded that either directly or indirectly, increased energy expenditure may ultimately lower survival in the reservoir or contribute to future mortality in the estuary or ocean. Lipid reserves also play a major role in eel migration as they stop feeding once silvering is completed (Olivereau & Olivereau 1997). Lipids present at the onset of the seaward migration should be sufficient for eel to cover the 5000–6000 km to the spawning grounds without feeding (van Ginneken & van den Thillart 2000; van Ginneken et al. 2005). This, even if the 6000 km trip burns 40–60% of the stored energy (van den Thillart et al. 2004). As for salmonids, we can expect that an increase in travel time will decrease body reserves and impair migration and breeding success of eels. However, silver eels are known to delay migration by up to a year to await favourable conditions (Vøllestad et al. 1994; Feunteun et al. 2000). Some may even resume feeding (Lee 1979; Feunteun et al. 2000). This flexible life strategy provides an alternative to migration when the biological costs of migration are too high during unfavourable conditions. However, in obstructed river systems where the 'quality' of eels is depressed by human impacts such as pollution or pathogenic threats (Robinet & Feunteun 2002), this plasticity could negate the benefits. For instance, in the Frémur system, cyanotoxin blooms (especially Microcystin-LR) are regularly observed in the Bois Joli reservoir in late summer because of eutrophication. Levels of Microcystin-LR, the most common and toxic compounds associated with cyanobacterial blooms, were recently analysed in fresh liver of 30 migrant silver eels caught at the onset of their seaward migration. Results showed that 50% of them were contaminated and that contaminated silver eels had significantly lower condition factors (Acou et al. 2008). Direct influence of toxins on eel metabolism and/or the increased energy demand required for the detoxification process are probably the two key factors that explain this effect (Acou et al. 2008). Overall, we believe that short (few months) or longer (1 year or more) migration delays above the Bois Joli reservoir impair migrating and breeding success of silver eels. Ongoing studies with PIT-tagged silver eels marked over the last 8 years are in progress to test the influence of migration delays on body condition. Future climate changes scenario predict a 1–7°C mean global temperature increase (Ficke et al. 2007). Human response to increased temperatures will lead to increased demand for water in reservoirs that will probably increase occurrence, in the case of the Frémur River, of late overflow years. In the context of climate changes, the influence of migration delays seems to be a key issue that must be urgently pursued for European eel conservation in obstructed river systems.

As observed elsewhere (Todd 1981; Haraldstad et al. 1985; Hvidsten 1985; Vøllestad et al. 1986; Haro 1991; Boubée et al. 2001) in the present study silver eels generally migrate when the water temperatures decrease. However, the variability explained by water temperature in the Frémur R. was very weak (6%) because of the important interannual variability of overflow periods. Only the addition of a second Wolf trap upstream part of the Bois Joli reservoir could have allowed us to more clearly analyse the influence of temperature on the onset of the migration. Vøllestad et al. (1986) who made a 10 years survey of seaward migration of eels in a Scandinavian river suggested that water temperature could influence the seaward migration, with low mean temperature during summer and autumn provoking an early departure. We could not test this hypothesis with the available data for the Frémur R. However, the important seasonal variability of migration periods observed in the Frémur R. provides some information on the range of temperature to which silver eels are subjected during their migration. In Scandinavian countries, minimum and maximum threshold beyond which the silver eel migration stops varies between 4 °C (Vøllestad et al. 1994) and 14 °C (Hvidsten 1985). In Spain, the temperature range varies between 10 and 16 °C (Lobon-Cervia & Carrascal 1992), similar to that of *A. rostrata* in Virginia, North America (between 9 and 13 °C according to Euston et al. 1997). In New Zealand, the seaward migration of *A. australis* and *A. dieffenbacchii* is reported to end below 11 °C (Boubée et al. 2001) but has been recorded as ranging from 7 to 19 °C (Todd 1981). Other studies have also shown that 6 °C is critical for enhancing general activity in eels, 10 °C for initiating migrations of eels larger than 260 mm (Naismith & Knights 1988; White & Knights 1997; Feunteun et al. 2003; Chadwick et al. 2007). However, migrating silver eels of the Frémur R. were captured at temperatures ranging from 4 to 23 °C, the largest reported in the literature. However, most of the migration (76.5% of captures) occurred between 6 and 10 °C. These results from the Frémur R. do not support the hypothesis that a temperature threshold initiates the seaward migration as it has been suggested by Haraldstad et al. (1985). On the contrary, our results show that eels are able to migrate over a very wide temperatures range (from 4 to 23 °C). Nevertheless, as suggested by Vøllestad et al. (1986), it is possible that water temperature act as a long-term factor that controls the period of physiological preparation of the migration such as the metamorphosis between yellow and silver eels.

Various studies have indicated that the migratory activity is highest during the second half of the lunar cycle, i.e. between the last quarter and the new moon (Frost 1950; Lowe 1952; Todd 1981; Deelder 1984). We found no such correlation and our results do not support Boëtius (1967) suggestion of an endogenous migration rhythm based on the lunar cycle. The importance of luminosity on the migratory activity of eels is supported by the daily migration patterns which show that migrations essentially occur at night (Deelder 1984; Haraldstad et al. 1985). Furthermore, in a recent laboratory study, Durif (2003) concluded that the effect of the moon on the migratory activity of the silver eels acts probably dependent on luminosity, not on an endogenous rhythm. Consequently, high light levels during the full moon could conceivably inhibit migrations whereas all the factors susceptible of causing low light levels (night, cloud layer and new moon) could facilitate it (Durif 2003). Similar influence of light on others diadromous fishes such as the smolts of Atlantic salmons *Salmo salar* is well established (Hansen & Jonsson 1985).

Rainfall and water discharge markedly affects the seaward migration of silver eels (Frost 1950; Lowe 1952; Deelder 1984; Vøllestad et al. 1986; Jonsson 1991; Chadwick et al. 2007). In the Frémur R., the autumn floods allow the filling of the Bois Joli water reservoir and then eventually allow it to overflow (Legault et al. 2003). In parallel, autumn floods causes migrant eels to accumulate in the reservoir until the dam overflows. Although Chadwick et al. (2007) observed autumn migration peaks when river flows were low several other have shown that a rapid increase in river flow in autumn stimulate the onset of silver eels migration (Vøllestad et al. 1986, 1994; Behrmann-Godel & Eckmann 2003). Captures we obtained in the periods before the Bois Joli Dam overflowed, (i.e. eels issuing from the reach between the dam and the trap) were mostly between August and December, the most important rainy period of the year (A. Acou, unpublished data). During overflow period, our results confirmed that the rain events (increase or decrease of rainfall), increasing river discharge and decreasing atmospheric pressure significantly increased the captures of migrant silver eels in the Wolf trap of Pont es Omnes. However, a rainfall does not always follow atmospheric depressions. These results suggest that hydro-dynamical movements are essential so that settled silver eels can orientate and swim over the Bois Joli Dam. During their migration, silver eels generally swim along the river bed to gain the most benefit from water currents (Jonsson 1991; Tesch 2003). In deeper water such as in the Bois Joli reservoir where the movements of water are buffered, only an important increase of rainfall and/or river flow associated with atmospheric depressions, acting as a flush, facilitates the escapement of silver eels. The most important captures we made were all obtained between 6 and 9 days after the overflow period began. This result suggest that both opening of the migration pathway (water level ≥28.20 m) and hydro-dynamical movements in the reservoir (increasing river discharge and rainfall) are necessary to allow silver eels to carry on their downstream migration in the Frémur R.

In conclusion, we have shown that silver eel migration in the Frémur catchment is highly dependent of the hydraulic management of the Bois Joli Dam. This dam causes an accumulation of silver eels that arise not only from upstream reaches but also from the reservoir itself. Apart from a minor number of silver eels that are able to find the minimum flow discharge pipe present at the Bois Joli Dam most silver eels remain trapped in the reservoir and are not able to pass downstream until the dam is filled and flows pass over weir. The consequence of this migration delay is not known but telemetry and other studies have shown that obstacles can cause a temporary end to the migration and even a reversion of silver eels to the yellow eel stage causing them to miss a favourable environmental window (Behrmann-Godel & Eckmann 2003; Durif et al. 2003, 2005). Furthermore, in the Frémur catchment, a long-term study of PIT-tagged silver eel led between 1996 and 2004 has shown that the fate of about 70% of the silver eels tagged above the Bois Joli reservoir remains unknown (Acou 2006). These lost eels have presumably either settled upstream of the dam or have died. Further studies should be undertaken to determine the fate of these eels so the full impact of reservoirs on European eels can be better quantified.

One management option which would allow silver eels to safely escape from the Frémur catchment is the removal of the Bois Joli Dam. However, this option is unrealistic given the county's growing water needs. Development of effective means of providing downstream passage is therefore a more acceptable option. Re-establishing free movement for migrating fish began with the development and construction of upstream fish passage facilities. Development of effective facilities for downstream migrations is often more difficult and complex and as a consequence is not as advanced as those concerning upstream fish passage (Larinier 2001). Recent studies with surface bypasses in New Zealand (Watene & Boubée 2005; Boubée & Williams 2006) have shown promising results and it would be valuable to determine if this technique can be used to pass European eels on the Frémur and other dams and weirs.

Acknowledgements

The authors would like to thank two anonymous reviewers for their constructive comments. We also express our sincere thanks to J. Boubée (NIWA, New Zealand) for its valuable comments and improvement of English style throughout the manuscript. This study was funded by the 'Fédération de Pêche et de Protection des Milieux Aquatiques d'Ille-et-Vilaine', the 'contrat de plan Poissons Migrateurs', and various regional and local councils. The surveys and samplings were organised and operated by the company FISH PASS.

References

Acou, A. 2006. Bases biologiques d'un modèle pour estimer la biomasse féconde de l'anguille européenne en fonction des recrues fluviales et du contexte de croissance: approche comparative à l'échelle de petits bassins versants, Ph.D. thesis. France: University of Rennes 1, 315 pp. http://www.diadfish.org/francais/documents_f.htm. Last accessed on 12 February 2008.

Acou, A., Feunteun, E., Laffaille, P. & Legault, A. 2000. Catadromous migration dynamics of European eel (*Anguilla anguilla*, L.) in a dammed catchment. Verhandlungen internationale Verein der Limnologie 27: 1–4.

Acou, A., Boury, P., Laffaille, P., Crivelli, A.-J. & Feunteun, E. 2005. Towards a standardized characterization of the potentially migrating silver European eel (*Anguilla anguilla*, L.). Archiv für Hydrobiologie 164: 237–255.

Acou, A., Poizat, G. & Crivelli, A.-J. 2006. Errors in ocular index measurements in European eel *Anguilla anguilla*. Ecology of Freshwater Fish 15: 578–582.

Acou, A., Gabriel, G., Laffaille, P. & Feunteun, E. (in press). Differential production and condition indices of premigrant eels (*Anguilla anguilla*) in two small Atlantic coastal catchments of France. In: Casselman, J. & Cairns, D., eds. Eels at the edge. Bethesda, MD: American Fishery Society, Symposium 58.

Acou, A., Robinet, T., Lance, E., Gerard, C., Mounaix, B., Brient, L., Le Rouzic, B. & Feunteun, E. 2008. Evidence of silver eels contamination by microcystin-LR at the onset of their seaward migration: what consequences for their breeding potential? Journal of Fish Biology 72: 753–762.

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.

Behrmann-Godel, J. & Eckmann, R. 2003. A preliminary telemetry study of the migration of silver European eel (*Anguilla anguilla* L.) in the River Mosel, Germany. Ecology of Freshwater Fish 12: 196–202.

Berg, R. 1986. Fish passage through Kaplan turbines at a power plant on the River Neckar and subsequent eel injuries. Vie Milieu 36: 307–310.

Boëtius, J. 1967. Experimental indication of lunar activity in European silver eels, *Anguilla anguilla* (L.). Meddelelser fra Danmarks Fiskeri-og Havundersogelser 6: 1–6.

Boubée, J.A.T & Williams, E.K. 2006. Downstream passage of silver eels at a small hydroelectric facility. Fisheries Management and Ecology 13: 165–176.

Boubée, J.A., Mitchell, C.P., Chisnall, B.L., West, D.W., Bowman, E.J. & Haro, A. 2001. Factors regulating the downstream migration of mature eels (*Anguilla* spp.) at Aniwhenua Dam, Bay of Plenty, New Zealand. New Zealand Journal of Marine and Freshwater Research 35: 121–134.

Budy, P., Theide, G.P., Bouwes, N., Petrosky, C.E. & Schaller, H. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. North American Journal of Fisheries Management 22: 35–51.

Chadwick, S., Knights, B., Thorley, J.L. & Bark, A. 2007. A long-term study of population characteristics and downstream migrations of the European eel *Anguilla anguilla* (L.) and the effects of a migration barrier in the Girnock Burn, north-east Scotland. Journal of Fish Biology 70: 1535–1553.

Congleton, J.L., Wagner, T., Evavold, J., Fryer, D. & Sun, B. 2002. Evaluation of physiological changes in migrating juvenile salmonids and effects on performance and survival. Report to the U.S. Army Corps of Engineers, contract DACW68-00-C-0031, Washington, DC: Walla Walla.

Cullen, P. & McCarthy, T.K. 2003. Hydrometric and meteorological factors affecting the seaward migration of silver eels (*Anguilla anguilla*, L.) in the lower River Shanon. Environmental Biology of Fishes 67: 349–357.

Deelder, C.L. 1984. Synopsis of biological data on the eel *Anguilla anguilla* (Linnaeus, 1758). Rome: FAO Fisheries Synopsis 80, FAO, 73 pp.

Durif, C. 2003. La migration d'avalaison de l'anguille européenne *Anguilla anguilla*: Caractérisation des fractions dévalantes, phénomènes de migration et franchissement des obstacles. Doctorat de l'Université en Ecologie Aquatique, Toulouse, France: Université de Toulouse II, 357 pp.

Durif, C., Gosset, C., Rives, J., Travade, F. & Elie, P. 2003. Behavioral study of downstream migrating eels by radiotelemetry at a small hydroelectric power plant. In: Dixon, D.A., ed. Biology, management and protection of catadromous eels. Bethesda, MD: American Fisheries Society, Symposium 33, pp. 343–356.

Durif, C., Dufour, S. & Elie, P. 2005. The silvering process of *Anguilla anguilla*: a new classification from the yellow resident to the silver migrating stage. Journal of Fish Biology 66: 1025–1043.

Escofier, B. & Pages, J. 1988. Analyses factorielles simples et multiples: objectifs, méthodes et interprétation. Paris: Dunod, 241 p.

Euston, E.T., Royer, D.D. & Simons, C.L. 1997. Relationship of emigration of silver American eels (*Anguilla rostrata*) to environmental variables at a low head hydro station. Atlantic, GA: Proceedings of the International Conference on Hydropower, 5–8 August 1997.

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

Feunteun, E., Acou, A., Guillouët, J., Laffaille, P. & Legault, A. 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., Acou, A., Laffaille, P. & Legault, A. 2000. European eel (*Anguilla anguilla*): prediction of spawner escapement from continental population parameters. Canadian Journal of Fisheries and Aquatic Sciences 57: 1627–1635.

Feunteun, E., Laffaille, P., Robinet, T., Briand, C., Baisez, A., Olivier, J.M. & Acou, A. 2003. A review of upstream migration and movements in inland waters by anguillid eels. Towards a general theory. In: Aida, K., Tsukamoto, K. & Yamauchi, K., eds. Eel biology. Tokyo: Springer-Verlag, pp. 191–213.

Ficke, A.D., Myrick, C.A. & Hansen, L.J. 2007. Potential impacts of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries 17: 581–613.

Frost, W.E. 1950. The eel fisheries of the river Bann, Northern Ireland and observations on the age of silver eel. Journal du Conseil Permanent International pour l'Exploration de la Mer 16: 358–393.

van Ginneken, V. & van den Thillart, G. 2000. Eel fat stores are enough to reach the Sargasso. Nature 403: 156–157.

van Ginneken, V., Antonissen, E., Müller, U.K., Booms, R., Eding, E., Verreth, J. & van den Thillart, G. 2005. Eel migration to the Sargasso: remarkably high swimming efficiency and low energy costs. Journal of Experimental Biology 208: 1329–1335.

van Ginneken, V., Durif, C., Paul Balm, S., Boot, R., Verstegen, M.W.A., Antonissen, E. & van den Thillart, G. 2007. Silvering of European eel (*Anguilla anguilla* L.): seasonal changes of morphological and metabolic parameters. Animal Biology 57: 63–77.

Gosset, C., Travade, F., Durif, C., Rives, J. & Elie, P. 2005. Tests of two types of bypass for downstream migration of eels at a small hydroelectric power plant. River Research and Application 21: 1095–1105.

Hansen, L.P. & Jonsson, B. 1985. Downstream migration of hatchery reared smolts of Atlantic salmon (*Salmo salar* L.) in the River Imsa. Aquaculture 45: 237–248.

Haraldstad, O., Vøllestad, L.A. & Jonsson, B. 1985. Descent of European silver eels, *Anguilla anguilla* L., in a Norwegian watercourse. Journal of Fish Biology 26: 37–41.

Haro, A.J. 1991. Thermal preferenda and behaviour of Atlantic eels (genus *Anguilla*) in relation to their spawning migration. Environmental Biology of Fishes 31: 171–184.

Haro, A.J., Castro-Santos, T. & Boubée, J. 2000. Behavior and passage of silver-phase American eels, *Anguilla rostrata* (LeSueur), at a small hydroelectric facility. Dana 12: 33–42.

Holmgren, K., Wickstrom, H. & Clevestam, P. 1997. Sex-related growth of European eel, *Anguilla anguilla*, with focus on median silver eel age. Canadian Journal of Fisheries and Aquatic Sciences 54: 2775–2781.

Hvidsten, N.A. 1985. Yield of silver eel and factors affecting downstream migration in the stream Imsa, Norway. Institute of Freshwater Research 62: 75–85.

Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. Nordic Journal of Freshwater Research 66: 20–35.

Laffaille, P., Acou, A., Guillouët, J., Mounaix, B. & Legault, A. 2006. Patterns of the silver eels (*Anguilla anguilla* L.) sex ratio in the Frémur catchment. Ecology of Freshwater Fish 15: 583–588.

Larinier, M. 2001. Environmental issues, dams and fish migration. In: Marmulla, G., eds. Dams, fish and fisheries. Opportunities, challenges and conflict resolution. Rome, Italie: FAO fisheries technical paper no. 419, pp. 45–89.

Lee, T.W. 1979. Dynamique des populations d'anguilles *Anguilla anguilla* (L.) des lagunes du bassin d'Arcachon. Thesis. Montpellier, France: University of Montpellier.

Legault, A., Acou, A., Guillouët, J. & Feunteun, E. 2003. Survey of downstream migration of silver eels through discharge pipe on a reservoir dam. Bulletin Français de la Pêche et de la Pisciculture 368: 43–54.

Lobon-Cervia, J. & Carrascal, M. 1992. Seasonal timing of silver eels in a Cantabrian stream. Archiv für Hydrobiologie 125: 121–126.

Lowe, R.H. 1952. The influence of light and other factors on the seaward migration of the silver eel (*Anguilla anguilla* L.). Journal of Animal Ecology 21: 275–309.

Moriarty, C. & Dekker, W. (eds.) 1997. Management of the European eel. Fisheries Bulletin 15: 110.

Naismith, I.A. & Knights, B. 1988. Migrations of elvers and juvenile European eels, *Anguilla anguilla* L., in the River Thames. Journal of Fish Biology 33: 161–175.

Olivereau, M. & Olivereau, J.M. 1997. Long-term starvation in the European eel: general effects and responses of pituitary growth hormone-(GH) and somatolactine-(SL) secreting cells. Fish Physiology and Biochemistry 17: 261–269.

Pankhurst, N.W. 1982. Relation of visual changes to the onset of sexual maturation in the European eel, *Anguilla anguilla L*. Journal of Fish Biology 21: 417–428.

Plumb, J.M., Perry, R.W., Adams, N.S. & Rondorf, D.W. 2006. The effect of river impoundment and hatchery rearing on the migration behavior of juvenile steelhead in the lower Snake river, Washington. North American Journal of Fisheries Management 26: 438–452.

Robinet, T. & Feunteun, E. 2002. Sublethal effects of exposure to chemical compounds: a cause for the decline in Atlantic eels? Ecotoxicology 11: 265–277.

Ryan, B.A., Smith, S.A., Butzerin, J.M. & Ferguson, J.W. 2003. Relative vulnerability to avian predation of juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary, 1998–2000. Transactions of the American Fisheries Society 132: 275–288.

Schmidt, J. 1922. The breeding places of the eel. Philosophical Transactions of the Royal Society of London 211: 179–208.

Sokal, R.R. & Rohlf, F.J. 1989. Biometry. New York: Freeman and Company.

Tesch, F.-W. 2003. The eel. 5th edn. Oxford: Blackwell Science, pp. 416.

van den Thillart, G., van Ginneken, V., Körner, F., Heijmans, R., van der Linder, R. & Gluvers, A. 2004. Endurance swimming of European eel. Journal of Fish Biology 65: 312–318.

Todd, P.R. 1981. Timing and periodicity of migrating New Zealand freshwater eels (*Anguilla* spp.). New Zealand Journal of Marine and Freshwater Research 15: 225–235.

Travade, F. & Larinier, M. 1992. La migration de dévalaison: problèmes et dispositifs. Bulletin Français de la Pêche et de la Pisciculture 326: 165–176.

Vøllestad, L.A., Jonsson, B., Hvidsten, N.A., Naesje, T.F., Haraldstad, O. & Ruud-Hansen, J. 1986. Environmental factors regulating the seaward migration of European silver eels (*Anguilla anguilla*). Canadian Journal of Fisheries and Aquatic Sciences 43: 1909–1916.

Vøllestad, L.A., Jonsson, B., Hvidsten, N.A. & Naesje, T.F. 1994. Experimental test of environmental factors influencing the seaward migration of European silver eels. Journal of Fish Biology 45: 641–651.

Watene, E.M. & Boubée, J.A.T. 2005. Selective opening of hydroelectric dam spillway gates for downstream migrant eels in New Zealand. Fisheries Management and Ecology 12: 69–75.

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.

Wickström, H., Westin, L. & Clevestam, P. 1996. The biological and economic yield from a long-term stocking experiment. Ecology of Freshwater Fish 5: 140–147.

Zaugg, W.S., Prentice, E.F. & Waknitz, F.N. 1985. Importance of river migration to development of seawater tolerance in Columbia River anadromous salmonids. North American Journal of Aquaculture 51: 33–47.