Environmental determinism of year-to-year recruitment variability of European eel *Anguilla anguilla* in a small coastal catchment, the Frémur River, north-west France

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The influence of environmental factors (mainly the river flow) on the year-to-year variability of European eel *Anguilla anguilla* fluvial recruitment in a small coastal catchment, the Frémur River (north-west France) was examined. A comprehensive survey of catches from fixed traps at two weirs located at 4·5 km (Pont es Omnes Dam) and 6·0 km (Bois Joli Dam) above the river mouth was carried out between 1997 and 2004. Young pigmented elvers (mean ± s.d. total length, 133·7 ± 29·6 mm) were recruited in eel-passes from February to October, but the main runs followed a modal curve from April to September with a peak centred in May to June. Catches varied greatly between years, from 381 to 26 765 elvers. For each trap, a positive linear relationship between monthly mean river flow that preceded the maximal intensity of captures and annual total catches was observed. These relationships explained 73·1% ($P < 0.01$) and 89·0% ($P < 0.001$) of the year-to-year variability of the recruitment observed in the Pont es Omnes and Bois Joli traps respectively. A significant increase in river flow at the beginning of the migration peak would thus trigger a greater proportion of *A. anguilla* settled in the estuary and in the downstream zone of the Fremur River to begin their freshwater colonization. The physicochemical roles of changes in river discharge in stimulating upstream migration are discussed. It is concluded that fluvial recruitment in the Fremur River is mainly determined by environmental factors.

Key words: habitat saturation; river flow; river recruitment; year-to-year variability.

INTRODUCTION

The eels *Anguilla* spp. are catadromous species that migrate between oceanic and continental waters during their life cycles. They are ubiquitous fish species of great commercial and ecological importance, which colonize coastal, estuarine and freshwater habitats (Tesch, 2003). Recruitment of the European eel *Anguilla anguilla* (L.) has declined considerably since the 1970s (Moriarty & Dekker, 1997; ICES, 2006). Likewise, decline in recruitment of other eel species such as the American eel *Anguilla rostrata* (Lesueur) (Dutil *et al*., 1989), the Japanese eel *Anguilla japonica* Temminck & Schlegel (Ringuet *et al*., 2002) or the New Zealand longfin eel *Anguilla dieffenbachii* Gray (Hoyle & Jellyman, 2002) have been observed. Recruitment and its associated variability, influences not only eel population size (*A. anguilla*: Parsons *et al*., 1977; Vøllestad & Jonsson, 1988; *A. rostrata*: Casselman *et al*., 1997) and structure (*A. anguilla*: Laffaille *et al*., 2005, 2006), but also stability and genetic composition as it has been shown for other species (*Lepomis macrochirus* Rafinesque: Cargnelli & Gross, 1996). In this context, elucidating the factors that determine the eel recruitment variability is essential for both ecological and conservation purposes.

At the end of their oceanic migration, anguillid leptocephali metamorphose into transparent glass eels which migrate into estuaries using passive tidal transport (McCleave & Kleckner, 1982; Gascuel, 1986). Some may enter fresh water in their first year, others remain in estuarine or coastal waters until they mature and emigrate as anguillid silver eels, others may migrate between habitats in different years (Daverat *et al*., 2006). Anguillid glass eels entering rivers undergo a transition phase as they adjust to fresh water (Ciccotti *et al*., 1993; Birrel *et al*., 2000), metamorphose into the pigmented elver stage (Elie *et al*., 1982) and start feeding (Bardonnet & Riera, 2005). This transition phase can last from a few days to a few weeks depending primarily on temperature and salinity conditions (Edeline & Elie, 2004; Briand *et al*., 2005). Some older anguillid yellow eels may even migrate upstream once they have reached a size at which sexual maturation begins (White & Knights, 1997*a*, *b*). All these pigmented anguillid eels originating from different cohorts that each year actively cross the tidal limit and start colonizing freshwater habitats form the river recruitment.

Recent experimental studies suggest that the river-oriented migratory behaviour of *A. anguilla* may be controlled by interacting physiological and environmental factors. For instance, low condition *A. anguilla* glass eels may preferentially colonize marine and estuarine habitats, while high condition fish may head towards freshwater habitats (Edeline *et al*., 2006). Moreover, low water temperature (10° C) significantly decreased both locomotor activity and preference for fresh water in *A. anguilla* glass eels as compared to higher temperature (18° C). Evidence of great individual plasticity, which could reveal further possibilities of expressing different behaviours according to biotic and abiotic conditions, however, were observed in the experiments of Imbert *et al*. (2008). Densities in these experiments were deliberately kept below threshold values that induced density-dependent escapement, thus this behaviour could be representative of an estuary below a saturation density.

In the field, the tendency to migrate upstream into fresh water after the *A. anguilla* glass eel stage varies greatly between ages and individuals (Naismith & Knights, 1988; White & Knights, 1997*a*, *b*; Feunteun *et al*., 2003). Moreover, the number of migrant *A. anguilla* which colonize fresh water varies greatly between years (Feunteun *et al*., 2003) and is probably related to interactions between density-dependent (*i.e*. number of *A. anguilla* glass eels and elvers in the estuary and older fish in the downstream parts of the river) and density-independent (*i.e*. environmental variables) factors. Naismith & Knights (1988), however, suggest that the environmental conditions which influence the brackish and freshwater transition phase of young *A. anguilla*, rather than the total number of elvers in the estuary, could be a cause of the recruitment variability. In French Atlantic estuaries, newly recruited *A. anguilla* glass eels are observed almost all year long, but the main run follows a modal curve from December to March with a peak occurring in February to March (Gascuel *et al*., 1995; Desaunay *et al*., 1996; Laffaille *et al*., 2007). It is therefore during this period that the environmental variables are likely to stimulate the brackish and freshwater transition and the start of upstream migration to fresh water.

Among relevant environmental factors, freshwater discharge and water temperature have been most frequently observed as influencing recruitment of *A. anguilla* (Tongiorgi *et al*., 1986; Tosi *et al*., 1990; White & Knights, 1997*b*; Edeline *et al*., 2006), *A. japonica* (Chen *et al*., 1994) and *Anguilla australis* Richardson (McKinnon & Gooley, 1998) glass eels and *A. rostrata* elvers (Jessop, 2003) from estuaries to rivers. Moreover, they also control river entry and upstream migration of migratory fish species such as Atlantic salmon *Salmo salar* L. (Jonsson *et al*., 2007). This study examined the influence of environmental factors (water temperature and river discharge) on the year-to-year variability of river recruitment in the Frémur River, a small coastal river system typical of the north-western French Atlantic coast's numerous hydrosystems. Moreover, whether environmental factors act equally on all young *A. anguilla* or preferentially on different age cohorts were also explored.

MATERIALS AND METHODS

STUDY SITE

The Frémur River is a small river in northern Brittany (France) which opens into the English Channel next to Saint Malo (48°32′ N; 2°04′ W). The catchment area is *c*. 60 km^2 and the overall length of the river and tributaries is 45 km, with 17 km attributed to the mainstem. The channel slope varies between 0·1 and 2·0% with an average of 0·6%, and the tidal limit is at the Roche Good mill (Fig. 1). No surveys of *A. anguilla* glass eel abundance in the estuary have been carried out.

The watershed contains two dams (Pont es Omnes and Bois Joli, Fig. 1), which completely blocked upstream fish migration until they were equipped with specific eel pass-traps to restore *A. anguilla* upstream migration and monitor *A. anguilla* recruitment (Legault, 1992). The Pont es Omnes is a 5 m high dam located 4·5 km from the estuary. The Bois Joli Dam, located 6 km upstream from the tidal limit, was built in 1991 and creates a 3×10^6 m^3 reservoir for drinking water. In Brittany, the presence of such dams is rather common as 27 water reservoirs of $>0{\cdot}5 \times 10^6$ m^3 in river catchments have been listed (http://eaubretagne.fr/articles/les-retenues-artificielles). Impoundments formed by the two dams reduce velocity and increase depth, thereby creating aquatic communities dominated by lentic water species [bream *Abramis brama* (L.), roach *Rutilus rutilus* (L.), rudd *Scardinius erythrophtalmus* (L.), tench *Tinca tinca* (L.), pike *Esox lucius* L. and zander *Sander lucioperca* (L.)]. Wetted area above the Pont es Omnes Dam totals 59·9 ha, including 5·3 ha of running waters and 54·6 ha of still waters above the two dams. Overall, the Fremur River provides a wide range of habitats from high-velocity streams of the 'trout zone' to lentic waters of the 'bream zone' in downstream areas.

EEL-PASS TRAPS

The Pont es Omnes Dam was equipped in late 1996 with a combined eel-pass trap. The eel pass consists of two ramps with bristle substrata that turn through 180° at a small resting pool. Above the upper ramp, where the pass crosses the dam crest, there is a 1m long horizontal stretch of channel with a rough pebble substratum. The attraction flow that helps *A. anguilla*

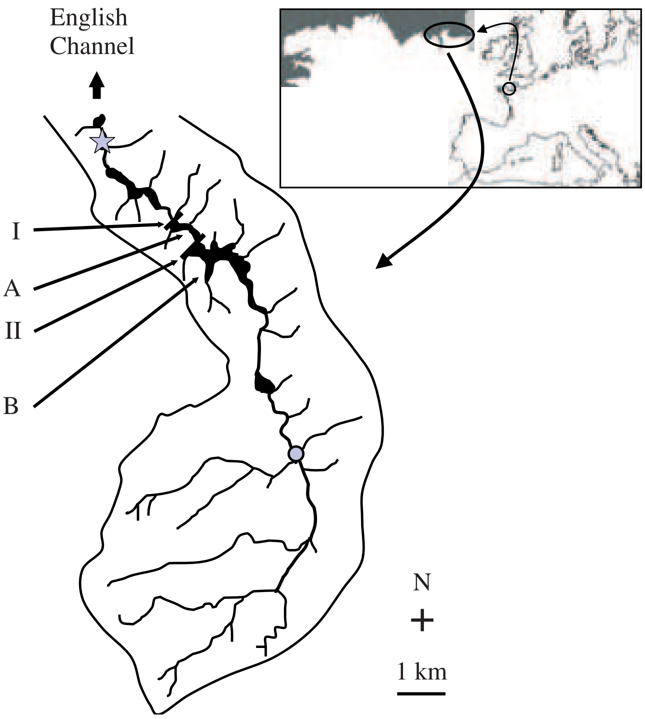

FIG. 1. Location and characteristics of the Frémur River catchment area (48°32′ N; 2° 04′ W). Bars indicate the location of the two major dams equipped with eel passes designed to reinstate upstream migration: I, Pont es Omnes trap (4·5 km from the sea); II, Bois Joli Dam (6·0 km from the sea) equipped with an eel lift. A, Pont es Omnes Reservoir; B, Bois Joli Reservoir. ☆, the tidal limit (Roche Good mill); ○, location of the gauging weir station.

to locate the pass and the flow within the pass itself is a gravity supply controlled by a sluice gate and fed from the retained level in the head pond. At the resting pool, the fish can be diverted using a third ramp which leads to a trap, or allowed to continue up to the crest of the dam. For the duration of the study, the trap facility was used and the upper pass ramp was dry. The Bois Joli Dam was equipped in 1992 with an eel lift, located near the compensation water spillway. The supply pipes for flow augmentation and attraction penetrate through the dam wall and take surface water from above the dam. The lift uses two flights of bristle-substratum ramps to lift the fish through a short hydraulic head to fall into a hopper in its ‘collect position’. The hopper is hauled to the crest of the dam by an electric winch where a lever mechanism opens the plug and releases the *A. anguilla* above the dam. During the study period, all ascending fish were trapped with a net before their release into the reservoir.

Comprehensive surveys of Pont es Omnes and Bois Joli pass traps were conducted from January 1997 to December 2004 (*i.e.* over eight upstream migration seasons). Over this period, the traps were inspected once every 3 days on average, and every day during migration peaks. Due to vandalism that led to a dysfunction of the eel pass and *A. anguilla* poaching during the migration peak, total annual catches observed at the Bois Joli trap in 1999 ($n = 5995$) represented a minimum and were not representative of a true time series. As it was not possible in this year of surveying to collect accurate data, the 1999 value was omitted and not considered in analyses. After this incident, security at the Bois Joli trap was reinforced to minimize potential damages due to vandalism.

All *A. anguilla* sampled were anaesthetized with clove oil (Walsh & Pease 2002) and measured [total length (L_T) to the nearest mm]. Migrants were classified as unpigmented ‘glass eels’ or pigmented juveniles, according to the macroscopic classification of Elie *et al.* (1982). A sample of 73 *A. anguilla* (mean ± S.D. $L_T = 141{\cdot}1 \pm 56{\cdot}0$ mm, range = 77–310 mm) caught in the Bois Joli trap in 1998 was aged by examination of the saggital otoliths. Otoliths were extracted and prepared (Mounaix & Fontenelle, 1994) to calculate the continental age (number of years in fresh water) of the fish by counting the number of annuli present after the entrance into fresh water, which is marked by a double ring. Otoliths that did not display an annual growth ring outside the elver centre were assigned to the river year-class 0+ year (Naismith & Knights, 1988). Growth rate was estimated as L_T per age and was expressed in mm year^{-1}. With the exception of samples that were used for ageing, fish were allowed to recover in cool, well-oxygenated water for *c*. 15 min before being released in the water above the dams.

ENVIRONMENTAL VARIABLES AND DATA ANALYSES

Daily river temperature (° C) was recorded with a data logger set at 1 m depth near the Pont es Omnes trap. Daily mean river discharge (Q, m^3 s^{-1}) was calculated from hourly records obtained at the upstream gauging weir (Fig. 1). Downstream, water level at the Pont es Omnes Reservoir was measured at each trapping session and river discharge was estimated using the following relation: $Q_{peo} = 0{\cdot}4 \times 2{\cdot}7 \times \sqrt{(2 \times 9{\cdot}81)} \times 0{\cdot}01\ [(W_L - W_{LD})]^{1{\cdot}5}$ where Q_{peo} (m^3 s^{-1}) is the river discharge observed at Pont es Omnes Reservoir, and W_L and W_{LD} are the water level and water level difference respectively. A significant positive relationship between Q_{peo} and Q was observed (linear regression: $n = 737$, $Q_{peo} = 0{\cdot}910Q + 0{\cdot}051$, $r^2 = 0{\cdot}84$, $P < 0{\cdot}001$), indicating that *A. anguilla* in the lower river and estuary are exposed to the river discharge measured at the upstream gauging station. Because the daily river flow series measured at the gauging weir (*v*. Pont es Omnes) presented no gap over the whole study period, Q was used to explore trap catches and river discharge relationships.

Short time-scale analyses of environmental factors (river temperatures and the possibilities of co-correlations with discharges at different time lags) and recruitment were considered using multiple regression analysis. Results, however, showed that catch data were poorly explained by river discharge and temperature on a daily (maximum time lags considered = 7 days; all $r^2 < 0{\cdot}05$), weekly (maximum time lags considered = 7 weeks; all $r^2 < 0{\cdot}09$) and monthly (maximum time lags considered = 3 months, all $r^2 < 0{\cdot}21$) basis. As a result, analyses were focused on an annual analysis of environmental factors and recruitment. Year-to-year variability observed between January and April, *i.e.* the most important months for *A. anguilla* glass eel arrival in the estuary (Gascuel *et al*., 1995; Desaunay *et al*., 1996), was far greater for river water discharge [coefficient of variation (C.V.) = 0·80, range: 0·07–1·51 m^3 s^{-1}] than for river water temperature (C.V. = 0·33, range: 4·16–16·23° C) (Fig. 2). Thus, further analyses were focused on river discharge, examining the relationships between annual recruitment as a dependent variable (Y) *v*. the independent variable of mean monthly river discharge recorded during the month prior to maximum catches in traps. The latter (from April to June) corresponds to the latest arrivals of *A. anguilla* glass eels in the Frémur Estuary and also includes both the brackish and freshwater transition and the start of upstream migration into fresh waters. Linear regressions were used to fit the relationships.

RESULTS

ANNUAL CATCHES

The average annual numbers of ascending *A. anguilla* recorded at Pont es Omnes and Bois Joli traps over the entire study period were 9895 and 9090 respectively. Numbers of ascending *A. anguilla* caught in Pont es Omnes decreased significantly (annual slope of −34%; $r = -0{\cdot}974$; $P = 0{\cdot}001$) between 1998 and 2003 but increased in the next years (Fig. 3). No such temporal trend was found in the Bois Joli trap mainly because the annual catch observed in 1999 was underestimated due to vandalism and theft, as noted earlier. Overall, an important annual recruitment variability was observed in both the Pont es Omnes (C.V. = 0·78, range: 2049–21 825 fish) and Bois Joli (C.V. = 0·95, range: 381–26 765 fish) traps.

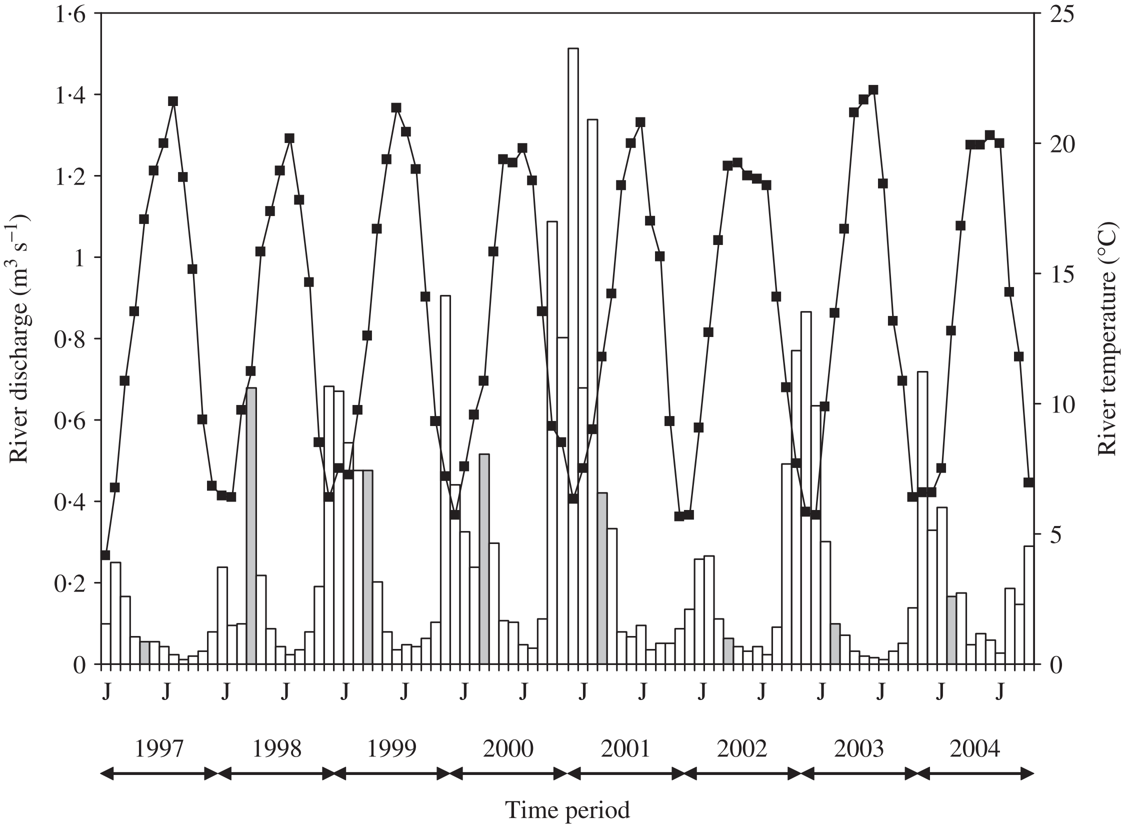

FIG. 2. Monthly trends in Frémur River discharge [□; ▒, mean river discharge recorded during the first month that precedes the *Anguilla anguilla* immigration peak of the year in Pont es Omnes (range: May–June)] and water temperature at the Pont es Omnes Dam (–■–) between January 1997 and December 2004.

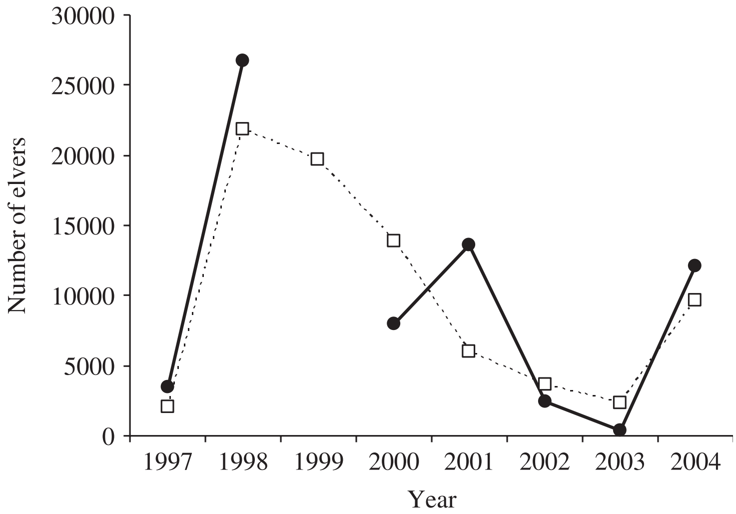

FIG. 3. Annual catches of migrant *Anguilla anguilla* elvers caught at Pont es Omnes (□) and Bois Joli (●) Dams from 1997 to 2004.

RECRUIT CHARACTERISTICS

Anguilla anguilla captured in traps ranged in L_T from 60 to 560 mm in Pont es Omnes, and from 58 to 1097 mm in Bois Joli (Fig. 4). In both traps, no *A. anguilla* glass eels were found, and the smallest fish caught were young pigmented *A. anguilla* $\geq$ stage VII. Modal L_T ranged from 110 to 140 mm in Pont es Omnes, and from 100 to 120 mm in Bois Joli. Each year, L_T structures of ascending fish caught were significantly different (Kolmogorov–Smirnov test, all $P < 0{\cdot}001$) between Pont es Omnes and Bois Joli (Fig. 4). Over the study period, the number of fish $\leq$ 120 mm was mean $\pm$ S.D. $2{\cdot}1 \pm 1{\cdot}8$. times greater in the Bois Joli than in the Pont es Omnes trap. Inversely, fish >120 mm were on average $4{\cdot}6 \pm 3{\cdot}8$ times higher in the Pont es Omnes than in the Bois Joli trap. In both traps, population structures were dominated by elvers (fish $\leq$ 180 mm), which represented $94{\cdot}3 \pm 3{\cdot}5\%$ and $98{\cdot}0 \pm 1{\cdot}4\%$ of total catches over the study period in the Pont es Omnes and Bois Joli traps respectively. These fish were mainly dominated by 0+ year (mean $\pm$ S.D. $60{\cdot}0 \pm 5{\cdot}9$ and $80 \cdot 4 \pm 9{\cdot}7\%$ of total catches over the study period in Pont es Omnes and Bois Joli traps respectively) and 1+ year ($34{\cdot}1 \pm 4{\cdot}9\%$ in Pont es Omnes and $17{\cdot}2 \pm 8{\cdot}9\%$ in Bois Joli) river year classes (Fig. 5). The results indicate a mean annual growth increment of 48·1 mm within the limits of observed ages (from 0+ to 2+ years).

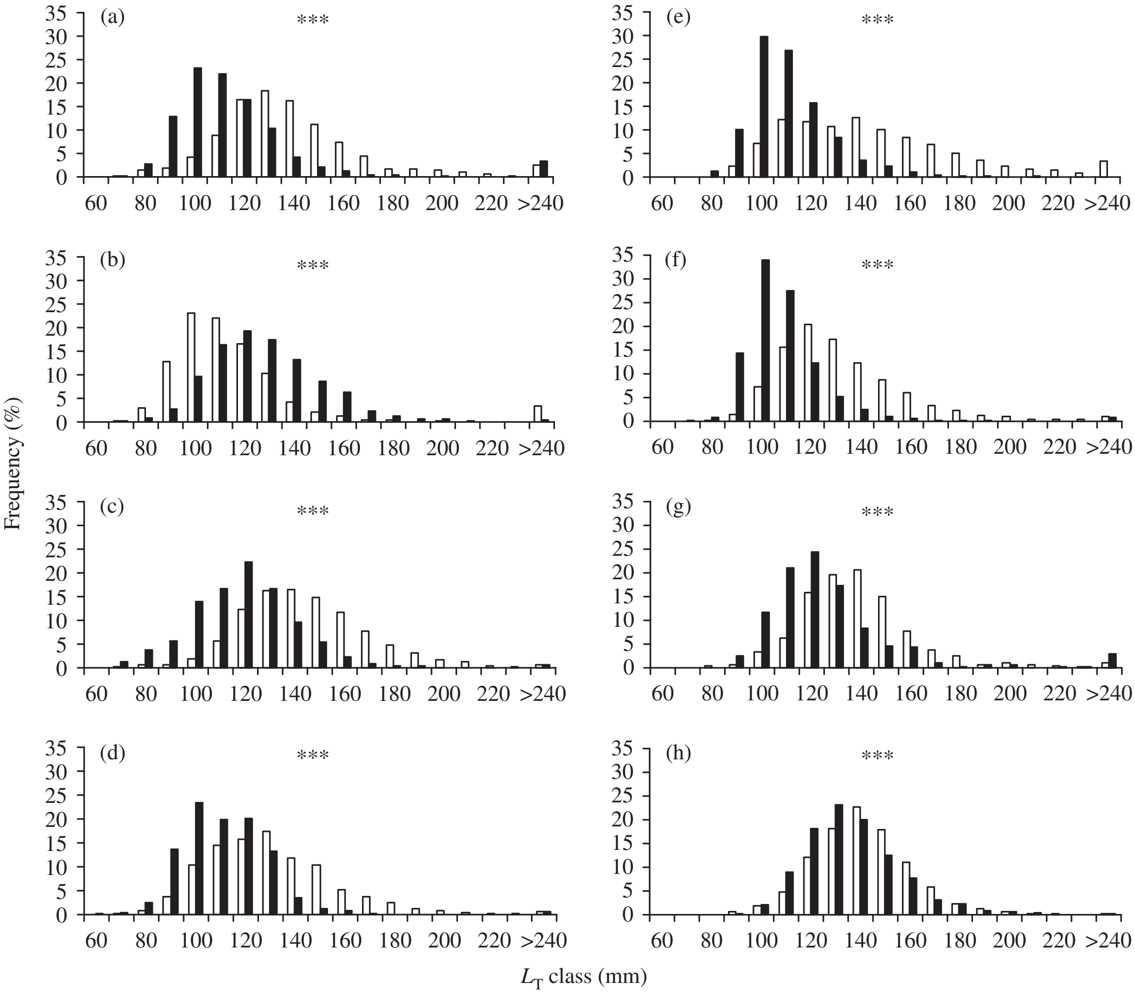

FIG. 4. The total length (L_T) class frequency of *Anguilla anguilla* recruits taken at Pont es Omnes (□) and Bois Joli (■) Dams from (a) 1997, (b) 1998, (c) 1999, (d) 2000, (e) 2001, (f) 2002, (g) 2003 and (h) 2004. Results of the Kolmogorov–Smirnov tests and their associated probabilities are shown as *** ($P < 0{\cdot}001$).

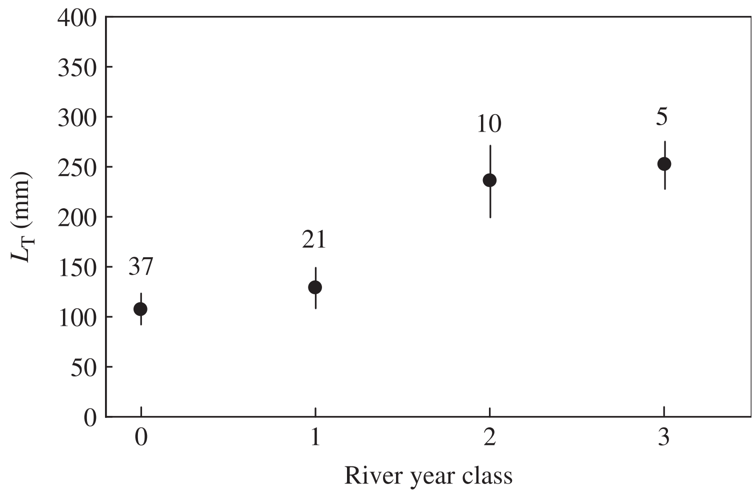

FIG. 5. The mean ± S.D. total length (L_T) of migrant *Anguilla anguilla* trapped at Bois Joli Dam against river year classes ($n = 73$). Numbers above each point indicate the total number of individuals caught in each year class.

UPSTREAM MIGRATION PHENOLOGY

The cumulative catches of *A. anguilla* in the traps are shown in Fig. 6. The catch patterns are characterized by a period of low captures in late winter or early spring, then one period of intense activity and finally a progressive fall to few catches at the beginning of the autumn. The timing of these periods, however, varies greatly between years as testified by the large S.D. In Pont es Omnes, migration peaks were generally observed in May except for the years 1997 and 2002 when they occurred in June. In Bois Joli, 25·0% of migration peaks were observed in May (years 1998 and 2004), 62·5% in June (years 1997, 1999, 2000, 2001 and 2002) and 12·5% in July (year 2003). Therefore, catch patterns observed between the two traps were similar, with a time lag of 1 month for the upstream site (Fig. 6). *Anguilla anguilla* elver catches were made over a broad temperature range of 3 to 26° C. *Anguilla anguilla* catches of 89·7 and 97·2%, however, were made when river temperatures were ≥12° C in Pont es Omnes and Bois Joli traps, respectively (Fig. 7).

EFFECT OF RIVER DISCHARGE ON RECRUITMENT

Annual recruitment was related to the mean river discharge recorded during the first month that preceded the migration peak of the year in Pont es Omnes (range: May–June) and Bois Joli (range: May–July). Fitted positive linear functions indicated that river discharge variability explained 73% ($P < 0·01$) and 89% ($P < 0·001$) of the variations of total catches observed in Pont es Omnes and Bois Joli respectively (Fig. 8). When only the river year-class 0+ was considered, the river discharge variability explained 77% ($P < 0·01$) and 92% ($P < 0·001$) of this year class catches in Pont es Omnes and Bois Joli, respectively. For the river year-class 1+ annual catches, the variability explained by river discharge dropped to 59% ($P < 0·05$) and 60% ($P < 0·05$) in both traps.

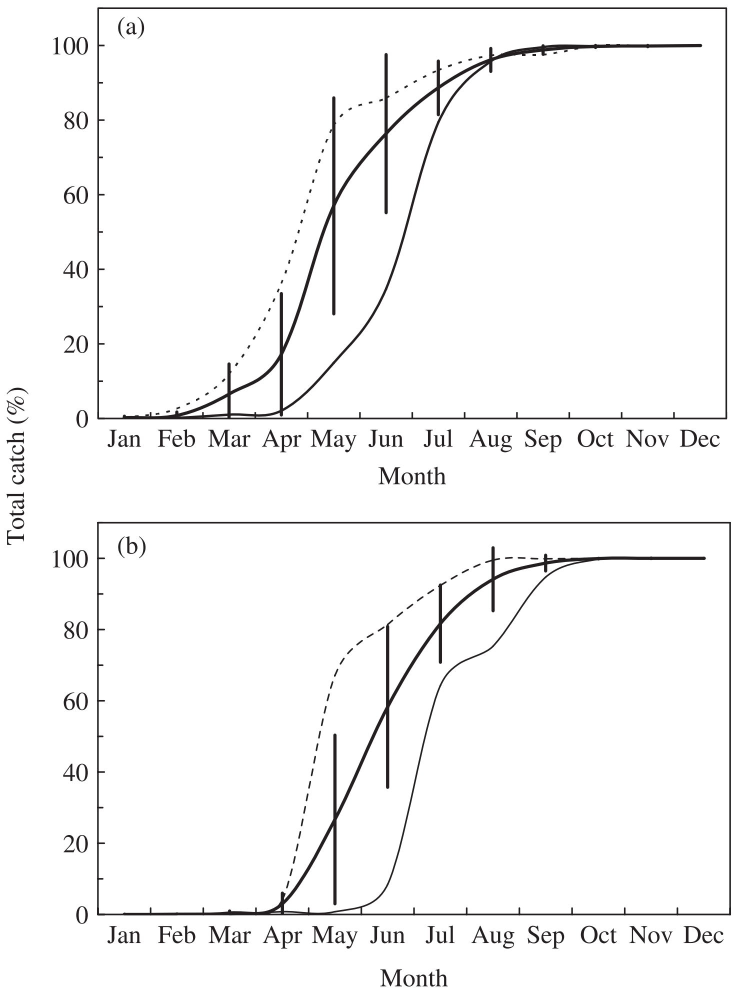

FIG. 6. The mean ± S.D. cumulative percentage of total catch of *Anguilla anguilla* recruits with month at (a) Pont es Omnes and (b) Bois Joli observed from 1997 to 2004. The ranges of migration pattern are shown: ..., earliest migration timing observed in Pont es Omnes (year 2001) and Bois Joli (year 1998); —, the latest migration timing (1997 and 2003 in Pont es Omnes and Bois Joli respectively).

DISCUSSION

The analysis of the L_T structure captured at Pont es Omnes and Bois Joli showed that nearly all (>95%) *A. anguilla* implicated in river recruitment were <180 mm, which corresponds principally to fish from the river year-classes 0+ and 1+. This result confirmed that recruits in the Frémur River were principally *A. anguilla* elvers that had recently carried out their brackish and freshwater transition and started to pigment, but also older fish that may have remained for 1 year in the estuary or in the downstream part of the catchment before their freshwater colonization. Each year, the L_T structures of *A. anguilla* observed in Pont es Omnes and Bois Joli traps were significantly different, with a higher number of small (≤120 mm) recruits captured at the Bois Joli trap. This result was contrary to expectations given the anguillid catadromous life cycle, where a decrease in density from the tidal limit to the upstream habitat is normally linked to an increase in average L_T with respect to distance to sea (Feunteun *et al.*, 1998; Ibbotson *et al.*, 2002). Spatio-temporal dynamic colonization of young (0+ year) recruits between the two dams was analysed (Acou, 2006) *via* a large-scale mark–recapture study of recruits, using

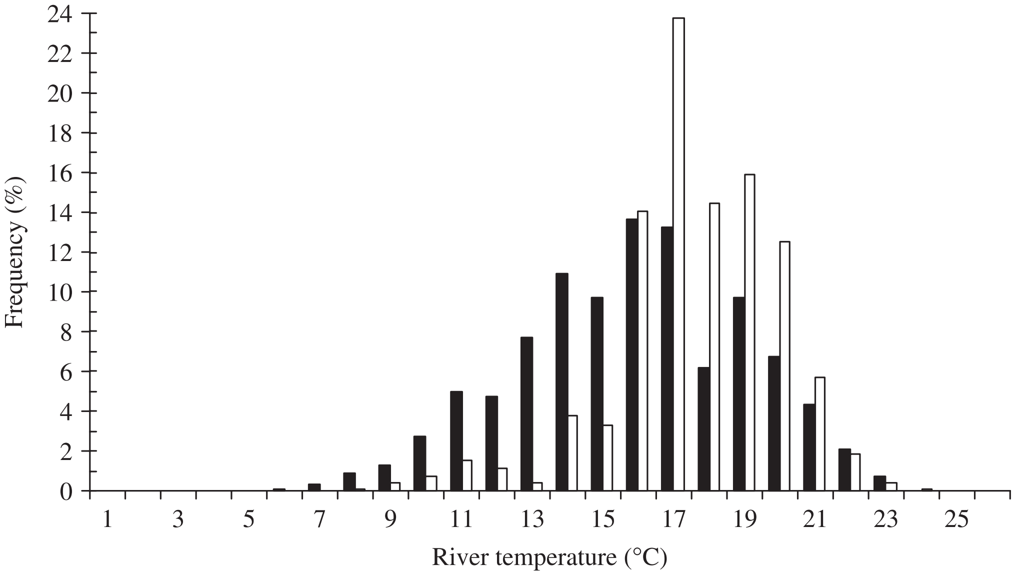

FIG. 7. Frequency distribution of *Anguilla anguilla* elvers captured at different river temperature classes from traps at Pont es Omnes (□; $n = 79\ 160$) and Bois Joli (■; $n = 72\ 719$).

fast balneation in calcein for marking (Alcobendas *et al.*, 1992). Results revealed a selectivity problem at the Pont es Omnes pass trap with respect to the smallest (≤120–140 mm) fish because many were able to climb the wall and cross the dam without passing through the pass trap (A. Acou, pers. obs.). Also, size-dependent migratory behaviours in the Pont es Omnes Reservoir may have affected the results (Acou, 2006). Given this gear selectivity with respect to the smallest *A. anguilla*, it is likely that the use of raw total catches at Pont es Omnes may lead to underestimation of both total catches and year-to-year variability. No such selectivity issue, however, has been observed at the Bois Joli trap. Therefore, it is likely that the Bois Joli trap collected the smaller individuals that the Pont es Omnes trap missed, suggesting that the Bois Joli trap provided more accurate estimates of recruitment, and its associated temporal variability.

The pass traps generally provide accurate estimates of the relative number of migrant *A. anguilla*, their year-to-year variability and migration timing (Legault, 1994; White & Knights, 1997*a*, *b*; Knights & White, 1998). In this study, *A. anguilla* were recruited over a 9 month period that spanned from February to October. The migration peaks generally occurred in late spring or early summer (from May to July) in both traps, but an important interannual variability occurred as is often the case in other catchments (Naismith & Knights, 1988). In the Pont es Omnes trap, a significant decrease in total catch (annual slope of −34%) between 1998 and 2003 was observed. This trend is consistent with the continued drop in recruitment observed in Europe over several decades (Moriarty & Dekker, 1997; ICES, 2006). A clear increase of the 2004 catches (*i.e.* four times greater than those observed in 2003), however, was observed. This result may suggest that there is not a direct linear relation between *A. anguilla* glass eel recruitment in estuaries and fluvial recruitment and that environmental factors control upstream migration of young *A. anguilla* in fresh water.

The river discharge positively influences the annual number of migrant *A. anguilla* captured in the two pass traps. The mean monthly values of river discharge used in

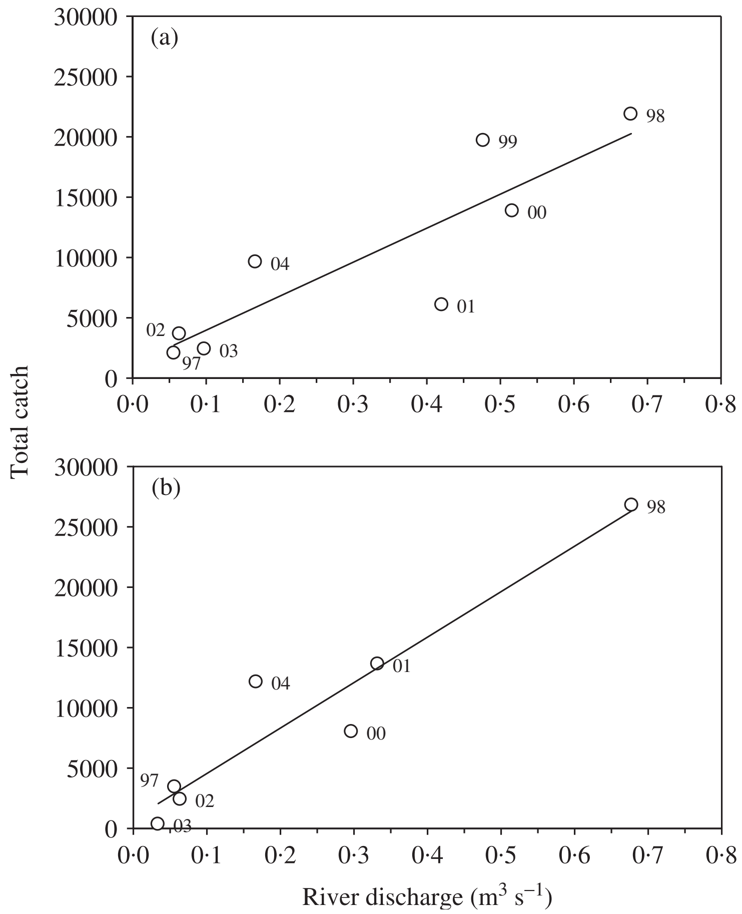

FIG. 8. Relationship between annual *Anguilla anguilla* recruitment and (a) mean river discharge recorded during the months prior to the maximum upstream migration activity (range: May–June) during the years 1997–2004 at Pont es Omnes and (b) mean river discharge recorded during the months prior to the maximum upstream migration activity (range: May–July) during the years 1997–2004 at Bois Joli. The curves were fitted by: (a) $y = 28\ 357x + 1117$ ($n = 8$, $r^2_{\text{adjusted}} = 0{\cdot}73$, $P < 0 \cdot 01$) and (b) $y = 37\ 707x + 762$ ($n = 8$, $r^2_{\text{adjusted}} = 0{\cdot}89$, $P < 0{\cdot}01$).

this study ranged according to the year between April and May in Pont es Omnes and April and June in Bois Joli, a period that corresponds to the start of upstream migration and when river temperature rarely falls below 12° C. Thus, an increase in river discharge at the start of the colonization process would incite a higher proportion of recruits present in the estuary or in the downstream habitats of the catchments to begin their upstream migration. This result supports the findings of Jellyman & Ryan (1983) who found a very strong positive relationship between river discharge and *Anguilla* spp. elver migration, except during low temperature periods. Moreover, Gandolfi *et al*. (1984) hypothesized that increasing river flow may have had a positive influence on upstream migration, but could come to no conclusions. The magnitude and timings of river discharge are dependent on the size of the catchment and channel flow characteristics. Thus, discharges may provide information to anguillid eels about the amount of habitat available and accessibility. There are many examples, however, where more anguillid eels enter a river system than can be supported by the local carrying capacity (Feunteun *et al*., 2003). Moreover, the relationship between flow and recruit catches in fresh water may have been due to olfactory cues that accompanied the increase in river flow. Anguillid eels have a very highly developed olfactory system and can detect odours at very low concentrations (Sorensen, 1986; Tosi & Sola, 1993; Tesch, 2003). Olfactory cues have been shown to help control the timing and duration of migration in both *A. rostrata* (Sorensen, 1986) and *A. anguilla* (Tosi *et al*., 1990; Briand *et al*., 2002). Fresh water from lakes and rivers has been demonstrated to increase activity rates of *A. anguilla* glass eels in aquaria, while charcoal filtered water does not (Creutzberg, 1961). Therefore, it is likely that years with higher spring river discharges (1998, but also 1999, 2000, 2001 and 2004) changed the composition of the dissolved components in the water and stimulated the migratory response of recruits.

The influence of environmental factors (mainly river temperature and river discharge) on the start of upstream migration of young pigmented anguillid eels is widely covered in the literature. Numerous studies have shown that anguillid glass eel migration and river recruitment are strongly dependent on water temperatures (Gascuel, 1986; Vøllestad & Jonsson, 1988; McGovern & McCarthy, 1992; Elie & Rochard, 1994; Martin, 1995; Jessop, 2003). In particular, anguillid glass eels in estuaries show a sharp decrease in migratory propensity below a threshold temperature of 10–12° C (Gascuel, 1986; McGovern & McCarthy, 1992; Jessop, 2003; Edeline *et al*., 2006; Sullivan *et al*., 2009). Moreover, the river flow generally has a strong negative influence on upstream migration (Sloane, 1984; Martin, 1995; Jessop, 2003), with an increase in current velocity immediately hindering the anguillid eels ability to migrate upstream, as has been observed experimentally (Sorensen, 1951; Barbin & Krueger, 1994). In the present study, young pigmented *A. anguilla* were captured in both traps at temperatures ranging between 3 and 26° C, but most of the migration (89·7 and 97·2% of total catches in Pont es Omnes and Bois Joli respectively) occurred when river temperatures exceeded 12° C. This result confirms that temperature is of most importance as a minimum threshold for migration of young pigmented *A. anguilla* elvers in the Frémur River, as it has been observed elsewhere (Gascuel, 1986; Vøllestad & Jonsson, 1988; McGovern & McCarthy, 1992; Elie & Rochard, 1994; Martin, 1995; White & Knights, 1997*b*; Jessop, 2003). No strong relationships, however, were found between short time-scale catches of river recruit abundance (on a daily, weekly and monthly basis) and environmental factors (mainly river temperature and the possibilities of co-correlations with discharge at different time lags). This result may suggest that short-term variability in water temperatures >10–12° C and river discharge have little effect on anguillid elver movement (Sorensen & Bianchini, 1986; Jessop, 2003). There were, however, some other factors not analysed in the present study. For example, tidal cycle and salinity have been shown to have a large influence of migratory choice of anguillid glass eels and elvers (Tosi *et al*., 1990; Cicotti *et al*., 1995; Edeline *et al*., 2005). Since this study was carried out entirely within fresh water, and the traps were not influenced by the tide, it is not possible to estimate the role that both factors may have played in influencing *A. anguilla* elver recruitment.

It can seem contradictory that on one hand, the river discharge greatly explains the magnitude of annual river recruitment (*i.e.* the annual pool of up-river migration candidates), yet on the other hand, no strong association between temporal pattern over short-time scales (on a daily, weekly and monthly basis) of *A. anguilla* elver abundance catches and environmental factors was found. It may be that once the high river discharges have stimulated the up-river migration in estuaries, social interactions occur. White & Knights (1997*b*) suggested that intraspecific competition and agonistic behaviour that increased with population density and biomass may encourage both dispersal and upstream migration. In the Frémur River, the estuarine recruitment is not known. The *A. anguilla* density observed in freshwater habitats located above the Bois Joli Reservoir that averaged $0{\cdot}40 \pm 0{\cdot}48$ individuals m^{-2} between 1995 and 2002 (Feunteun *et al*., 1998; Laffaille *et al*., 2003; Acou *et al*., 2009) were at the upper range of *A. anguilla* density estimates in French (Office National de l'Eau et des Milieux Aquatiques, pers. com.) and western European catchments (Moriarty & Dekker, 1997). These high abundance levels observed, probably due to the favourable location of the estuary for *A. anguilla* glass eel arrivals relative to the North Atlantic migration pathways (Kettle & Haines, 2006), the restoration of upstream migration (Laffaille *et al*., 2005), the low fishing pressure (no commercial fishery is present) and low avian predation mortalities on young *A. anguilla* by piscivorous birds (cormorants and ardeids are scarce in the study area), may indicate that strong competition behaviour of young recruits occurs in downstream areas of the Frémur River. Variations in river discharge explained yearly 0+ year catches (77 and 92% in Pont es Omnes and Bois Joli, respectively) better than 1+ year catches (*c*. 60% in both traps). Therefore, *A. anguilla* elver migration may proceed as a wave initiated by departures of these fish (mainly 0+ year) present in large numbers in estuaries towards freshwater reaches, causing older fish (mainly $\geqslant$ 1+ year) to move further upstream, with the wave progression being weakly dependent on environmental factors. In this context, speed of migration should be fast enough to ensure a rapid response to river flow events. The latter, calculated by dividing the number of days between supposed start of up-river migration and maximal catches in traps each year (*c*. 1 month) by the distance covered (*c*. 5 km from tidal limit to both traps), ranged between 0·15 and 0·20 km day^{-1}. This value is low compared to mean migration rate of pigmented *A. anguilla* elvers (0·64 km day^{-1}) in the non-tidal Rivers Severn and Avon (U.K.) observed by White & Knights (1997*a*). The present calculations, however, may be underestimated. Because anguillid elver migration is inhibited by increases in current velocity (Sorensen, 1951; Sloane, 1984; Barbin & Krueger, 1994; Martin, 1995; Jessop, 2003), it is likely that the start of the migration is later than predicted, and thus, that the travel period between estuary and trap is shorter. It is not possible, however, to make more accurate estimates of *A. anguilla* elver migration speed with the data available. Edeline *et al*. (2006) suggested that in the wild, low condition *A. anguilla* glass eels may preferentially colonize saltwater habitats, while high-condition fish may orientate towards freshwater habitats. This hypothesis cannot be tested with the data available. The relatively large mean annual growth rate for young *A. anguilla* in the Frémur River (48·1 mm, $year^{-1}$) compared to other similar western catchments (Adam, 1997), however, suggests that only high condition *A. anguilla* elvers have the capacity to colonize fresh water, especially when high levels of intraspecific competition occurs. Further studies should aim to directly test this hypothesis.

The migration of young anguillid eels is seasonal but is highly variable from year to year and only involves part of the population. This may reflect complex interactions between density-dependent and independent factors. Recent findings have revealed the existence of 'sea eels' which never enter fresh water (Daverat *et al*., 2006), suggesting a critical need for studies examining what factors govern the choice of anguillid glass eels and elvers to either enter estuaries and move upstream, or settle in coastal areas and never venture into freshwater habitats. The probable 'saturation' of the Frémur River (Feunteun *et al*., 2003; Acou, 2006) suggests that despite a probable decline in estuarine *A. anguilla* glass eel recruitment in recent years, as observed elsewhere in Europe, the proportion of fish that succeed in migrating upstream is important relative to available habitats. This proportion mainly depends upon environmental variability and in the Frémur River increases with the increasing river flow that occurs at the beginning of upstream migration. If *A. anguilla* glass eel recruitment continues to decline (ICES, 2006), it is likely that fluvial recruitment in the Frémur River will also decrease.

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