

Factors determining survival of European eels in two unexploited sub-populations

CLARISSE BOULENGER^{*†}, ANTHONY ACOU^{*}, OLIVIER GIMENEZ[‡], FABIEN CHARRIER[§], JULIEN TREMBLAY^{¶**} AND ERIC FEUNTEUN^{*}

^{*}UMR BOREA 7208, CNRS, IRD, UPMC – Service des stations marines du MNHN, CRESCO, Muséum National d'Histoire Naturelle, Dinard, France

[†]INRA, UMR 985, INRA-Agrocampus, Ecologie et Santé des Ecosystèmes, Rennes Cedex, France

[‡]Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, Campus du CNRS, Montpellier, France

[§]Fish Pass, Laillé, France

[¶]1036 UZE, Pôle GEST'AQUA, INRA, Rennes Cedex, France

^{**}Pôle GEST'AQUA, ONEMA, Rennes Cedex, France

SUMMARY

1. Estimating accurate age-specific survival probabilities and understanding the processes (density dependent or independent) that regulate this demographic parameter are fundamental to propose sustainable management options for the endangered European eel (*Anguilla anguilla*).
2. In the present study, we used extensive mark-recapture data sets (13 and 17 years) on eel >150 mm to estimate accurate natural survival probabilities of two eel sub-populations, from the Oir and Frémur rivers, western France, and then we analysed survival probabilities in relation to density-independent (temperature) and density-dependent factors to identify those causing survival variability.
3. The Frémur and Oir rivers are two small (<100 km²) river systems in close proximity (65 km apart). The Frémur River is a small river obstructed by dams with medium water quality, high eel recruitment and density (0.37 eel m⁻²), and a male dominant population; whereas, in the Oir River, low densities of eels were observed (0.04 eel m⁻²) and the sex ratio was skewed towards females. Furthermore, previous research suggested that the lotic habitats of the Frémur River have reached carrying capacity, whereas habitats in the Oir River are below habitat saturation.
4. In the Frémur River, there were significant spatial and temporal variations in the survival probabilities. However, survival probabilities observed in the Oir River were stable over time and space. The results highlight that the differences in the characteristics of the two systems and the two sub-populations prompt different responses to regulatory processes.
5. The contrasting pressures applied on these two sub-populations impact survival, which possibly lead to different life history strategies such as sex differentiation.

Keywords: European eel, Life-history characteristics, sex ratio, survival

Introduction

Estimates of accurate demographic parameters such as age-specific survival are fundamental to propose suitable sustainable environmental management methods, especially for endangered species (Caswell, 2000). The estimation of demographic parameters and identification of

the processes that influence these parameters may help predict the future dynamics of populations in the face of environmental changes and anthropogenic pressures. The factors influencing demographic parameters can be classified into two groups: density-independent (water flow, temperature, pollutants, dams, etc.) and density-dependent (essentially competition) factors. For the lat-

Correspondence: Clarisse Boulenger, INRA, UMR 985 INRA-Agrocampus, Ecologie et Santé des Ecosystèmes, 65 rue de Saint Briec, CS 84215, F-35042 Rennes Cedex, France. E-mail: clarisse.boulenger@rennes.inra.fr

ter, the effects on the size or growth of a population vary with the density of the population itself (Williams, Nichols & Conroy, 2002).

In fish populations, density-independent factors could act through direct or indirect effects. For example, some studies highlighted that temperature causes both an increase (by hastening body growth and reducing the duration of the freshwater phase at the optimum temperature; Vøllestad, 1992; Angilletta & Dunham, 2003) and a decrease (directly from the critical thermal temperature at which the fish dies) of survival. The effect of density dependence on demographic parameters could strongly regulate a population by decreasing survival, fecundity, and growth rates and; therefore, understanding density-dependent processes is crucial for practical applications such as conservation and harvest regulations (Hanski, Foley & Hassell, 1996; Sinclair & Pech, 1996; Drake, 2005). These processes are particularly important for populations when the system is near carrying capacity (defined as the maximum density or biomass that a habitat can sustain; Van Gils *et al.*, 2004) as limited resources (habitat or/and food) could result in enhanced intra-specific competition reducing growth and survival. However, these processes are often difficult to highlight as long-term data sets are required.

European eels (*Anguilla anguilla*) are catadromous, semelparous fish reproducing in the open ocean and spending most of their life in continental waters from recruits (glass eels or elvers) that colonise water courses until sub-adult silver eels that migrate back to the reproductive grounds in the Sargasso Sea (Tesch, 2003). In recent decades, the European eel population has declined drastically and the current glass eel recruitment has reached only 10% of the reference 1960–1979 period (ICES WGEEL, 2013). As a result, this species was listed as critically endangered in the IUCN Red List (Jacoby & Gollock, 2014). The European Commission has initiated an Eel Recovery Plan (Council Regulation no. 1100/2007) in an attempt to reduce anthropogenic mortality and maximise silver eel output from catchments. Stocking of juvenile eels to under-stock waterways has been identified as a method to increase spawning stock biomass (Josset *et al.*, 2015). However, identifying areas where stocking will be most successful and have the highest net benefit requires a comprehensive understanding of the factors influencing eel survival rates during the successive eel life stages.

Natural survival of eels is a major, but relatively unknown, factor in the population dynamics of eels. In a recent study, Bevacqua *et al.* (2010) applied principles of metabolic theory, which linked natural survival to body

mass and temperature, to estimate natural survival of the European eel. They first highlighted that eels inhabiting warm waters are potentially subject to a markedly lower survival as temperature accelerates all metabolic processes, therefore shortening the lifespan. Secondly, at a given temperature, the survival of a high-density eel stock is about three times lower than that of a low-density one (Bevacqua *et al.*, 2010), which is consistent with others local studies (e.g., Vollestad and Jonsson, 1988; De Leo & Gatto, 1996; Lobón-Cerviá & Iglesias, 2008). Thus, eel survival can be influenced in complex ways by both density-dependent and -independent processes (Noth, Francis & Jellyman, 2008; Bevacqua *et al.*, 2010, 2011) but further studies are still needed to disentangle the factors influencing eel survival in different environments (Knights, 2003). Furthermore, the regulation processes (density-independent or -dependent) could be different depending on the age and/or size of the individuals. For example, the diet of European eels shifts with increasing fish proportion as their size increases (Cucherousset *et al.*, 2011), suggesting that intra-specific competition for food could be size specific. It is therefore necessary to estimate age/size-specific survival to determine at which stage these processes regulate the population. Some studies highlighted that survival increases with age (De Leo & Gatto, 1995, 1996: age-specific annual mortality [1–15 years]; Lobón-Cerviá & Iglesias, 2008: cohort mortality and from age 2 to 4 mortality). However, when age-data were unavailable or unreliable, studies demonstrated that mortality also varied with size (Naim-Smith & Knights, 1990; Bisgaard & Pedersen, 1991).

In the current study, we analysed spatio-temporal variations in natural survival probabilities of two eel sub-populations in relation to density-independent (temperature, water flow) and -dependent factors. We used an extensive mark-recapture data set (13 and 17 years), on eels >150 mm, from sub-populations of the European eel in two small (<100 km²) river systems of Western France: Frémur (Brittany) and Oir (Normandy) rivers. In both sites, there was no commercial eel fishery, anglers did not target European eels, and, there were few cormorants and herons. Therefore, fishing pressure and predation mortality were negligible, and survival provided hereafter consisted of natural survival. Multistate capture recapture models were developed to estimate annual survival probabilities of five different stages (depending on sexual maturation and size: yellow eels with a size >300 mm, yellow eels between 301 and 450 mm, yellow eels with a size >451 mm, and resident and migratory silver eels) in each system. Both sites are in close proximity (65 km apart) and are affected by similar

regional environmental conditions (water temperature, hydrology, etc.). However, they differ in water quality, fish population, and eel population structure (density, recruitment, and sex ratio). In addition to these differences, differences in the inherent habitat carrying capacity of each system are suspected. Previous research suggested that the lotic habitats of the Frémur River have reached carrying capacity (Acou *et al.*, 2011) whereas the Oir River is possibly below habitat saturation. Considering the close proximity of the two systems and the important difference in population structure (density, recruitment, sex ratio), we expected higher eel survival in the low-density Oir River than in the higher-density Frémur River linked to density-dependent processes.

Methods

Study areas

The Frémur and Oir rivers are typical of the numerous small river systems in Western Europe. The Frémur is a small and low-gradient coastal river in Northern Brittany, which discharges into the English Channel near Saint Malo (2°06'W, 48°34'N; Fig. 1). The catchment area is approximately 60 km², and the distance from source to mouth is 46 km, with a 17 km main stem. The gradient ranges from 2% at the source (100 m altitude) to 0.1% near the mouth. Overall, the Frémur River provides a wide range of shallow (mean \pm SD = 0.5 \pm 0.2 m) and narrow

(2.2 \pm 0.9 m) habitats, from turbulent headwater streams with trout to lowland reaches downstream characteristic of bream habitats, together with lentic reservoirs. At roughly the same latitude (1°16'W, 48°37'N), 60 km eastward, the Oir is a small river tributary of the Sélune, and flows into Mont Saint Michel Bay (Fig. 1). The catchment area is 87 km², and the main stem is approximately 25 km long. The mean gradient is 1.1%.

In the Frémur, despite a medium water quality, high recruitment and density levels (0.37 eel m⁻²) of eels could be observed. In this system, the European eel is the most common species in terms of biomass and in the shallow (<1 m) habitats, males are dominant (>80%; study period: 1996–2013). By contrast, the Oir River is a tributary of the Sélune River and is known as a salmonid river (Baglinière, Marchand & Vauclin, 2005; Rivot *et al.*, 2008). In this system, low densities of eels were observed (0.04 eel m⁻²) and the sex ratio was skewed towards females (>90%; 2000–2013).

The Oir River is obstructed by only one weir, and the Frémur River is obstructed by two major dams (Pont es Omnes and Bois Joli) that were previously impassable until the construction of fish passes (Feunteun *et al.*, 1998). The highest Dam, at Bois Joli, is 14 m high and holds a 3 \times 10⁶ m³ reservoir. A lift for the upstream migration of eels was built in 1996. Upstream, three minor works, including a culvert under a road, a flow-gauging device, and a sill (step) beneath a bridge, have created temporary obstacles for eel migration, but are passable during periods of high flow (Feunteun *et al.*,

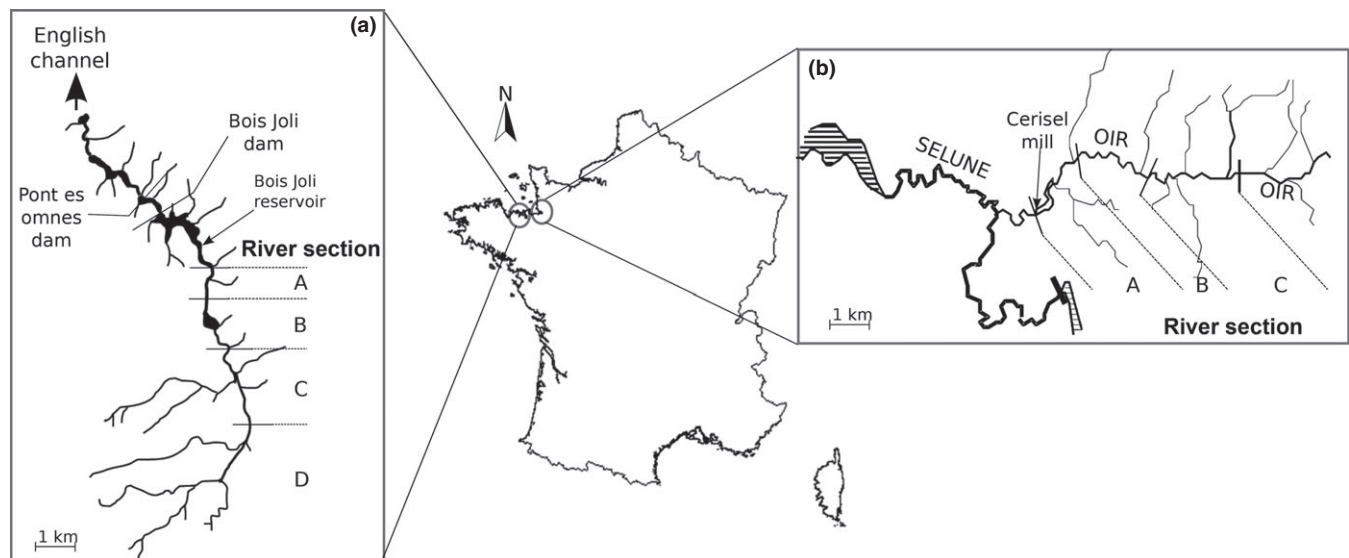


Fig. 1 Map of France, showing the location and configuration of the studied drainage basins: (a) The Frémur River, (b) the Oir River, and the different river sections studied.

1998). These three obstacles lead to an accumulation of eels downstream of the hydraulic works and very low densities immediately upstream of the obstacle (Feunteun *et al.*, 1998).

Sampling

Annually (between 1996 and 2012 in the Frémur, and between 2000 and 2012 in the Oir), two methods were used to sample eels in each river. Firstly, between September and October, growing and sub-adult eels were captured using electrofishing with a 'Heron' apparatus (Dream Electronique, Pessac, France) set at DC 300 V and 3 A, in different sampling sites along the longitudinal gradient of the rivers (between 15 and 32, and between 15 and 39 sampling sites per year for the Frémur and Oir rivers respectively). Most sites were sampled with a minimum of two successive removals. Additional removals (three or four) were made if necessary, until the catch per pass decreased by 75% or more between successive passes (Acou *et al.*, 2011). For our analyses, in both catchments, sampling sites were regrouped into river sections, to take into account the distance to the sea and the downstream–upstream productivity of each system. Four river sections were defined in the Frémur River by using temporary obstacles to migrating eels (Fig. 1; Feunteun *et al.*, 1998; Acou *et al.*, 2011). The three river sections of the Oir River were chosen based on the location of the principal tributaries of the river (Fig. 1).

Secondly, between September and February (depending on the rise in the level of the rivers), growing and sub-adult eels that leave the system were caught with a downstream trap placed at the Pont es Omnes Dam in the Frémur River and at the Cerisel water-mill in the Oir River (Fig. 1).

All captured eels were anaesthetised with clove oil (Walsh & Pease, 2002) and measured (total length, TL, to the nearest mm), weighed (total weight, TW, to the

nearest g) and their stage (yellow or silver eel) determined. Silver eels were identified by three criteria (Acou *et al.*, 2005; Acou, Poizat & Crivelli, 2006): the colour of the back and belly, the presence of a well-defined lateral line, and an ocular index (OI) ≥ 6.5 , according to Pankhurst's silvering threshold value (Pankhurst, 1982). If only two of the criteria (most often the lateral line and OI value) were met, the eel was considered a silver eel. If only one (generally the OI value) or none were met, the eel was regarded as yellow.

Eels caught during sampling with a length >150 mm, were individually marked with passive integrated transponder tags (Prentice, Flagg & McCutcheon, 1990; Table 1). For the newly marked and recaptured eels, individual information was recorded (TL, TW, stage, site, and date). After handling, the fish recovered for more than 15 min before being released at the site of capture.

Survival and transition probability estimates

For each system, multistate capture-recapture models with an annual time step were used to analyse the data (Lebreton *et al.*, 2009) and estimate annual survival (Φ), transition (w), and detection (P) probabilities. For the eels individually marked (1367 and 2356 marked eels in Frémur and Oir rivers, respectively), six different stages were created considering different ecological and behavioural characteristics (Baisez, 2001; Laffaille *et al.*, 2004; Acou *et al.*, 2011): Stage 1 (S_1) consisted of recently recruited elvers that colonised the river and sedentary growing yellow eels (yellow eels with a size <300 mm), stage 2 (S_2) (yellow eels between 301 and 450 mm) and stage 3 (S_3) (yellow eels with a size >451 mm) represented the potential reproductive status of future male or female silver eels, respectively). The resident and the migratory silver eels (individuals caught as silver eel in the sampling sites and in the downstream trap respectively) represented stage 4 (S_4) and 5 (S_5), respectively.

Table 1 Marking effort and number of eels recaptured in all the lotic habitats sampled since the beginning of the marking campaign in the Oir (2000–2012) and Frémur (1996–2012) rivers. × represents absence of marking and/or recapture sessions.

	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
The Frémur																	
Marked	356	231	82	8	150	87	67	44	×	×	×	×	103	69	80	47	43
Recaptured	0	77	22	22	32	17	33	28	22	6	1	5	0	23	20	24	18
The Oir																	
Marked	×	×	×	×	194	203	115	106	150	133	208	58	198	292	269	203	227
Recaptured	×	×	×	×	×	25	30	61	40	46	51	36	38	62	102	124	129

Individuals can enter in the population at any of these stages. Finally, D represented the dead eels.

The annual temporal dynamics of stages was determined by transition probabilities (w). The possible transition from a stage to another were fixed considering the growth rates observed in the Oir and Frémur rivers (mean: 19.1 mm year⁻¹, max: 93 mm year⁻¹, and mean: 20.9 mm year⁻¹, max: 134 mm year⁻¹, respectively). Then, eels from S_1 could stay in S_1 or change to S_2 , S_4 , or S_5 , eels from S_2 could stay in S_2 or change to S_3 , S_4 , or S_5 , eels from S_3 could stay in S_3 or change to S_4 or S_5 , eels from S_4 could stay in S_4 or change to S_5 . Migratory silver eels could only stay in the migratory silver eel stage (as they left the system), then the transition probability from S_5 to S_5 was fixed to 1. Transition probability from a stage to a smaller stage was fixed to 0. Similarly, as a silver eel could not return to a yellow eel stage, the transition probabilities from S_4 to S_1 , S_2 , or S_3 were fixed to 0. The full transition matrix was presented in Table 2. These transitions were conditional on survival probability (Φ) and stages were related to observations through detection probabilities (P). The survival matrix is presented in Table 3. We defined a set of candidate models, for each system, incorporating biologically relevant combinations of year, stages, and river section effects on survival, transition, and detection probabilities. Regarding temporal effects on survival and transition, we considered continuous effects to test for the influence of environmental conditions. We incorporated a river section effect to assess whether the localisation of eels influenced their survival and transition probabilities. Studies have shown that growth and body conditions near the estuary are often higher than in the upper reaches of a river catchment (Daverat *et al.*, 2006; Lasne *et al.*, 2008). Regarding recapture probabilities, we considered temporal effects, and because silver eels were supposed to be less sedentary than other stages due to their need to migrate downstream to the sea, we tested for the influ-

ence of stage. We incorporated these effects in each parameter (P , Φ and w) sequentially while constraints on remaining parameters were held constant. To develop the most suitable model, we firstly selected the most appropriate structure for P testing from the different effects individually. Once the main effect was determined, the remaining effects were included in an additive and interactive way to assess if one of these combinations was relevant and this process continued until no more effective model was selected. Secondly, we repeated the same procedure for Φ using the previously selected structure for P and finally for w using the structures for P and Φ selected in the previous steps. The most parsimonious model was selected, using the Akaike information Criterion (AIC; Burnham & Anderson, 2002). These analyses were performed using the software program E-SURGE (Choquet *et al.*, 2009a), and the quality of fit of the models (Pradel, Wintrebert & Gimenez, 2003), using the software program U-CARE (Choquet, Rouan & Pradel, 2009b). If time-dependent survival was identified, the effect of different parameters on time variation was investigated by performing an analysis of deviance (ANODEV) as described by Grosbois *et al.* (2008), using the statistics $F_{\text{test}_{\text{cst/co/t}}}$:

$$F_{\text{test}_{\text{cst/co/t}}} = \frac{\text{Deviance}(F_{\text{cst}}) - \text{Deviance}(F_{\text{co}})}{\tau - 1} \div \frac{\text{Deviance}(F_{\text{co}}) - \text{Deviance}(F_t)}{n - \tau}$$

With F_{cst} , the model with constant survival, F_t where survival was time-dependent, F_{co} where survival was determined by a linear relationship with the covariate, n the number of survival estimates obtained from the model F_t and τ the number of parameters required to describe the relationship between survival and the covariate. Effects of biotic and abiotic parameters were then tested, using the statistics $F_{\text{test}_{\text{cst/co/t}}}$ in Frémur and Oir river survival analysis and by applying the Bonferroni procedure for processing with the multiple

Table 2 Transition matrix for the two eel populations representing the possible transitions (w) from a specific eel life-stage (S_1 , S_2 , S_3 , S_4 , S_5) to another.

		To:					Dead
		S_1 : Yellow eel 150–300 mm	S_2 : Yellow eel 301–450 mm	S_3 : Yellow eel >450 mm	S_4 : Silver eel resident	S_5 : Silver eel migratory	
From:	S_1	$1 - \sum_{i=2}^5 w_{S_1 \rightarrow S_i}$	$w_{S_1 \rightarrow S_2}$	0	$w_{S_1 \rightarrow S_4}$	$w_{S_1 \rightarrow S_5}$	0
	S_2	0	$1 - \sum_{i=3}^5 w_{S_2 \rightarrow S_i}$	$w_{S_2 \rightarrow S_3}$	$w_{S_2 \rightarrow S_4}$	$w_{S_2 \rightarrow S_5}$	0
	S_3	0	0	$1 - \sum_{i=4}^5 w_{S_3 \rightarrow S_i}$	$w_{S_3 \rightarrow S_4}$	$w_{S_3 \rightarrow S_5}$	0
	S_4	0	0	0	$1 - w_{S_4 \rightarrow S_5}$	$w_{S_4 \rightarrow S_5}$	0
	S_5	0	0	0	0	1	0
	Dead	0	0	0	0	0	1

Table 3 Survival matrix for the two eel populations.

	Alive as S ₁	Alive as S ₂	Alive as S ₃	Alive as S ₄	Alive as S ₅	Dead
S ₁ : Yellow eel 150–300 mm	Φ_{S_1}	0	0	0	0	$1 - \Phi_{S_1}$
S ₂ : Yellow eel 301–450 mm	0	Φ_{S_2}	0	0	0	$1 - \Phi_{S_2}$
S ₃ : Yellow eel >450 mm	0	0	Φ_{S_3}	0	0	$1 - \Phi_{S_3}$
S ₄ : Silver eel resident	0	0	0	Φ_{S_4}	0	$1 - \Phi_{S_4}$
S ₅ : Silver eel migratory	0	0	0	0	Φ_{S_5}	$1 - \Phi_{S_5}$
Dead	0	0	0	0	0	1

test issue. For the significant covariates, the proportion of variance explained by the covariate using the R^2 statistic (Grosbois *et al.*, 2008).

Factors used to explain temporal survival variability

To explain temporal survival variability, different factors were tested. This analysis was only focused on the three yellow eel stages (S₁, S₂, and S₃).

Temperature. Sadler (1979) determined both upper and lower lethal temperatures for eels. They highlighted that the critical thermal maximum varied from 33 to 39 °C and that eels enter a state of torpor at temperatures varying from 1 to 3 °C. In the Oir River, water temperatures were recorded using a probe located downstream in the river. In the Frémur, daily river temperature (°C) was recorded with a data logger set at 1 m depth near the downstream trap. During our study period, water temperatures ranged from 0.95 to 25.8 °C with an average temperature of 13.05 °C in the Frémur River and from –1.8 to 21.7 °C with an average temperature of 11.9 °C in the Oir River, so eels never encountered the critical thermal maximum, but they could be affected by low temperatures. Therefore, we calculated the number of days when the water temperature was below 3 °C (ND 3) between two sampling sessions to determine the possible effect of these low temperatures on eel survival. Furthermore, water temperature could be used as a proxy of the primary productivity of the system (Morin, Lamoureux & Busnarda, 1999), then productivity and associated potential prey for eels should decrease with decreasing water temperatures, which could lead to decreased survival. To understand this possible effect, the mean water temperature between two sampling sessions was calculated (T_{mean}).

Density. As highlighted by previous studies, density could have a strong impact on survival (Lobón-Cerviá & Iglesias, 2008; Bevacqua *et al.*, 2010). For each sample site with more than two consecutive passes (between 25 and 31 sites and between 6 and 14 sites every year in Frémur and Oir rivers, respectively) using all individuals sampled, thanks to the depletion method used for the samplings, eel abundance was calculated using a weighted maximum likelihood model (Carle & Strub, 1978) and density (eels m⁻²) was calculated by dividing the estimated abundance by the surface area of the sampled site. Thus, the total density (regrouping all the stages) was estimated for each sampled site every year and the specific densities of the three yellow eel stages were estimated as the competition for food is size specific with their diets evolve with increasing proportions of fish as their size increases (Schulze *et al.*, 2004; Cucherousset *et al.*, 2011). The mean of all sampled site densities was used as the proxy of the total density of the system. Then, four variables were created: $dt_{t,\text{tot}}$ representing the total density (regrouping all the stages) of the system in the year t , and dt_{t,S_1} , dt_{t,S_2} , dt_{t,S_3} representing the total densities of S₁, S₂, and S₃, respectively, of the Frémur and Oir rivers for year t .

Recruitment. In small catchments such as the Frémur, major concentrations of glass eels recruited from the ocean are still found, presumably because of different currents, which are the principal vector for eel recruitment in Europe (Dekker, 2003; Bonhommeau *et al.*, 2010). Moreover, in such small rivers, young recruits may colonise the whole river in a single wave of upstream migration (Feunteun *et al.*, 2003). It is likely that such massive colonisation of rivers by recruits could induce important pressure on individuals already established and lead to decreasing inter- and intra-cohort survival. A fish-lift installed at the Bois Joli dam in the Frémur River enabled the passage and count of the total number of recruits entering the system (between 381 and 26765 recruits, coefficient of variation: 0.82) and their characteristics (size and stage). We tested if this highly variable number of recruits (Fig. 2) could explain the temporal survival variability of the in-stream eel population of the Frémur River. Such data are unavailable for the Oir River.

Results

Considering the model selected for each system, the goodness-of-fit test results strongly support that we could not reject the null hypothesis if the models fitted the data

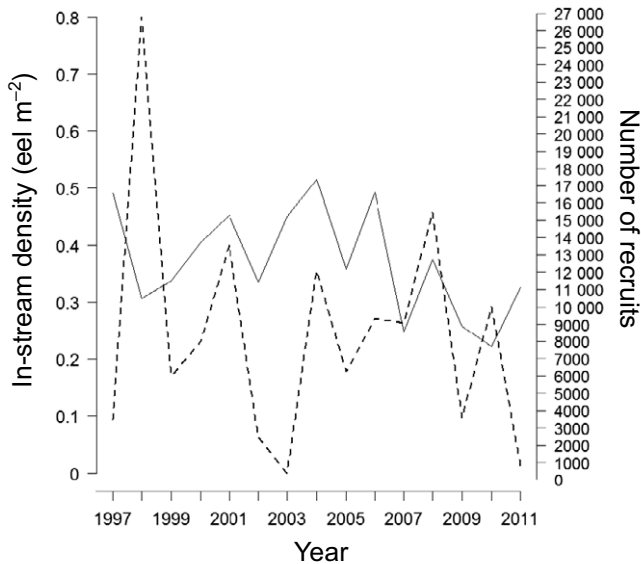


Fig. 2 Temporal variation in the in-stream density (eel m^{-2} ; dotted line) and recruitment (dashed line) of *Anguilla anguilla* in the Frémur River.

adequately (for the Frémur: $\chi^2 = 45.445$, d.f. = 85, $P = 1$; for the Oir: $\chi^2 = 97.243$, d.f. = 98, $P = 0.503$).

For both systems, the most suitable models predicted that detection probabilities varied according to stage and time. However, regarding the survival and transition probabilities, the main effects on these parameters differed (Tables 4 and 5).

In the Oir River, survival probabilities varied according to stage with an increase of survival with size ($S_1 = 0.60$, $S_2 = 0.85$, $S_3 = 0.80$; Fig. 3), but were constant in time and space (absence of river section effect). In the Frémur River, survival probabilities between the yellow eel stages were slightly different (on average $S_1 = 0.77$, $S_2 = 0.72$ and $S_3 = 0.81$; Fig. 4), but varied with marked fluctuation over the study period (between 0.29 and 0.99; Fig. 4). A decrease in survival probability was observed in 1998 (0.46), 2000 (0.55), and 2006 (0.46) (Fig. 4). Furthermore, survival probabilities varied spatially (on average in the downstream river section A: 0.71, B: 0.78, C: 0.68, and in the upstream river section D: 0.73; Fig. 4). Because the survival probabilities (for all the stages and all the river section) were estimated as 1 in 1999, a boundary of the domain of a probability, the estimates are unreliable for this particular year. Mean annual survival probability was lower in the Oir than in the Frémur River for S_1 (z -test (Lebreton *et al.*, 1992), $z = -2.032$, $P < 0.05$), whereas the mean annual survival probability was higher in the Oir than in the Frémur River for S_2 ($z = 6.780$, $P < 0.05$). No significant differ-

Table 4 Subset of models considered with AIC values for each set of parameters (detection, survival, and transition probabilities) for the Frémur. For each set of parameters best models are in bold. A ‘-’ stands for constant parameter. A ‘+’ is used when effect is additive whereas an ‘ \times ’ is used for an interaction. ΔAIC corresponds to the difference between the AIC value of the current model and the best model.

Parameter	Effect	AICc	$\Delta AICc$
Detection P	-	8483.8	327.8
	Time	8332.3	176.3
	State	8327.6	171.6
	State + Time	8307.7	151.7
	State \times Time	8323.0	167.0
	$F(S_1, S_2, S_3, S_4) \times \text{Time} + F(S_5)$	8403.7	247.7
	$F(S_1, S_2, S_3, S_4) + \text{Time} + F(S_5)$	8388.3	232.3
	$F(S_1, S_2, S_3, S_4) + F(S_5) \times \text{Time}$	8404.7	248.7
	$F(S_5) + \text{Time} + F(S_1, S_2, S_3, S_4)$	8388.3	232.3
	Survival Φ	-	8307.7
Time		8286.3	130.3
State		8220.3	64.3
River section		8282.2	126.2
State + River section		8197.3	41.3
State \times River section		8195.5	39.5
State + Time		8185.6	29.6
State \times Time		8245.9	89.9
State + Time + River section		8165.1	9.1
State + Time \times River section		8203.3	47.3
Transition ψ	-	8165.1	9.1
	State	8156.0	0
	Time	8161.2	5.2
	River section	8168.3	12.3
	State + Time	8164.8	8.8
	State \times Time	8273.5	117.5
	State + River section	8172.2	16.2
	State \times River section	8272.3	116.3

ence of S_3 mean annual survival was observed between the two systems ($z = 0.257$, $P = 0.80$).

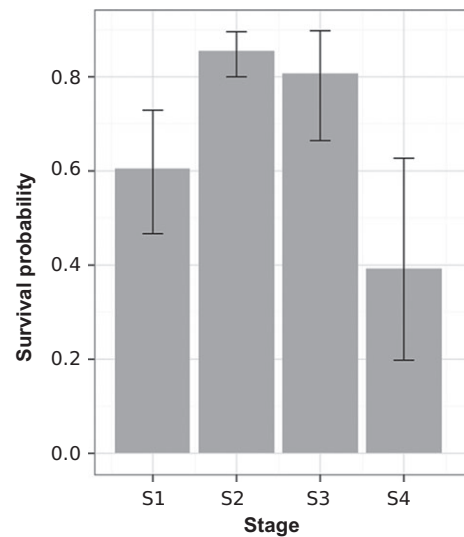
In the Oir River, transition probabilities were influenced by time and stage (Fig. 5), whereas in the Frémur River, transition from one stage to another varied with stages but was constant in time (Fig. 6). The mean annual transition probabilities from S_1 to stage S_2 and stage S_2 to S_3 were equivalent in the Oir and Frémur River ($z = -1.019$, $P = 0.308$; $z = -1.409$, $P = 0.159$, respectively). Furthermore, in the Oir River, few individuals from S_2 changed to a silver eel stage (average transition probabilities from S_2 to S_4 and S_5 : 0.02), whereas in the Frémur River, transition probability from S_2 to S_4 and S_5 was 0.20 (from S_2 to S_4 : $z = 2.934$, $P < 0.05$; from S_2 to S_5 : $z = 4.920$, $P < 0.05$).

For the Frémur data set, ANODEV revealed that no single covariate explained the temporal variability of survival significantly (Table 6, $P > 0.05$). In the Oir River, the most suitable model predicted that survival

Table 5 Subset of models considered with AIC values for each set of parameters (detection, survival, and transition probabilities) for the Oir River. For other details, see Table 4.

Parameter	Effect	AICc	Δ AICc	
Detection P	–	11468.9	175.1	
	Time	11447.5	153.6	
	State	11424.9	131.1	
	State + Time	11395.4	101.5	
	State \times Time	11357.2	63.4	
	$F(S_1, S_2, S_3, S_4) \times \text{Time} + F(S_5)$	11425.2	131.3	
	$F(S_1, S_2, S_3, S_4) + \text{Time} + F(S_5)$	11411.1	117.2	
	$F(S_1, S_2, S_3, S_4) + F(S_5) \times \text{Time}$	11398.4	104.5	
	$F(S_5) + \text{Time} + F(S_1, S_2, S_3, S_4)$	11398.0	104.1	
	Survival Φ	–	11357.2	63.4
Time		11359.1	65.2	
State		11307.6	13.7	
River section		11359.7	65.8	
State + River section		11311.0	17.1	
State \times River section		11313.7	19.9	
State + Time		11309.3	15.4	
State \times Time		11351.7	57.8	
Transition ψ		–	11307.6	13.7
		State	11304.9	11.0
	Time	11309.3	15.5	
	River section	11315.7	21.8	
	State + Time	11293.9	0	
	State \times Time	11365.1	71.3	
	State + River section	11309.6	15.7	
	State \times River section	11308.3	14.4	
	State + Time + River section	11295.3	2.4	
	State + Time \times River section	11295.8	2.9	

probabilities varied according to stage, but were constant in time and space. However, as results highlighted that there are still relatively large confidence intervals in the Oir River survival estimates (S_1 : 0.47–0.73, S_2 : 0.80–0.89, S_3 : 0.66–0.90), analyses were carried out to test if a model with a temporal covariate would outperform the constant model. Four reference time-dependent models were selected: $F_{t, \text{tot}}$ where survival probabilities of the three yellow eel stages (S_1, S_2, S_3) varied with time, F_{t, S_1} where only the survival probabilities of S_1 varied with time, F_{t, S_2} where only the survival probabilities of S_2 varied with time, F_{t, S_3} where only the survival probabilities of S_3 varied with time. Then, different covariates were incorporated into the selected time-dependent models ($F_{t, \text{tot}}, F_{t, S_1}, F_{t, S_2}, F_{t, S_3}$). Using the ANODEV and then the Bonferroni procedure for multiple tests, no single covariate explained a significant part of the survival considering the reference models $F_{t, \text{tot}}, F_{t, S_2}$, and F_{t, S_3} . For the model F_{t, S_1} , $dt_{t, \text{tot}}$ and dt_{t, S_1} explained a significant part of the survival ($P < 0.05$, Table 7). However, individually those covariates explained less than 0.01% of the deviance in the temporal variance of survival probabilities (Table 7). Therefore, no ecological relevant conclu-

**Fig. 3** Survival probabilities of the three yellow eel stages (S_1, S_2, S_3) and of the silver eel stage (S_4) in the Oir River. Error bars represented the 95% confidence interval.

sions could be made on the impact of the different covariates on survival due to the low explained variance.

The time-dependent reference model for the Frémur River was finally selected. In the Oir River, the results highlighted that the covariates explained a very small part of the temporal survival variability, but also that a model with a temporal covariate did not outperform the constant model (AIC difference, Table 5). Therefore, the most suitable model found for the Oir River was the constant model. Using those two models, we evaluated the mean annual natural survival probabilities observed for yellow eel stages in the Frémur and Oir river systems and found these to be 0.76 ± 0.18 and 0.75 ± 0.13 respectively.

Discussion

The survival estimates observed in the two systems are in the range of others values for European catchments such as the Imsa River in Norway (mean survival: 0.833 y^{-1} ; Vollestad & Jonsson, 1988) or the Esva River in Spain (0.621 y^{-1} ; Lobón-Cerviá & Iglesias, 2008). However, our major results show that their population dynamics differ to some extent, suggesting different responses to regulatory processes.

In the Frémur River, survival probabilities varied significantly along the water course. Previous studies on yellow European eels in river systems show that distance from the sea (Ibbotson *et al.*, 2002) and/or the presence of

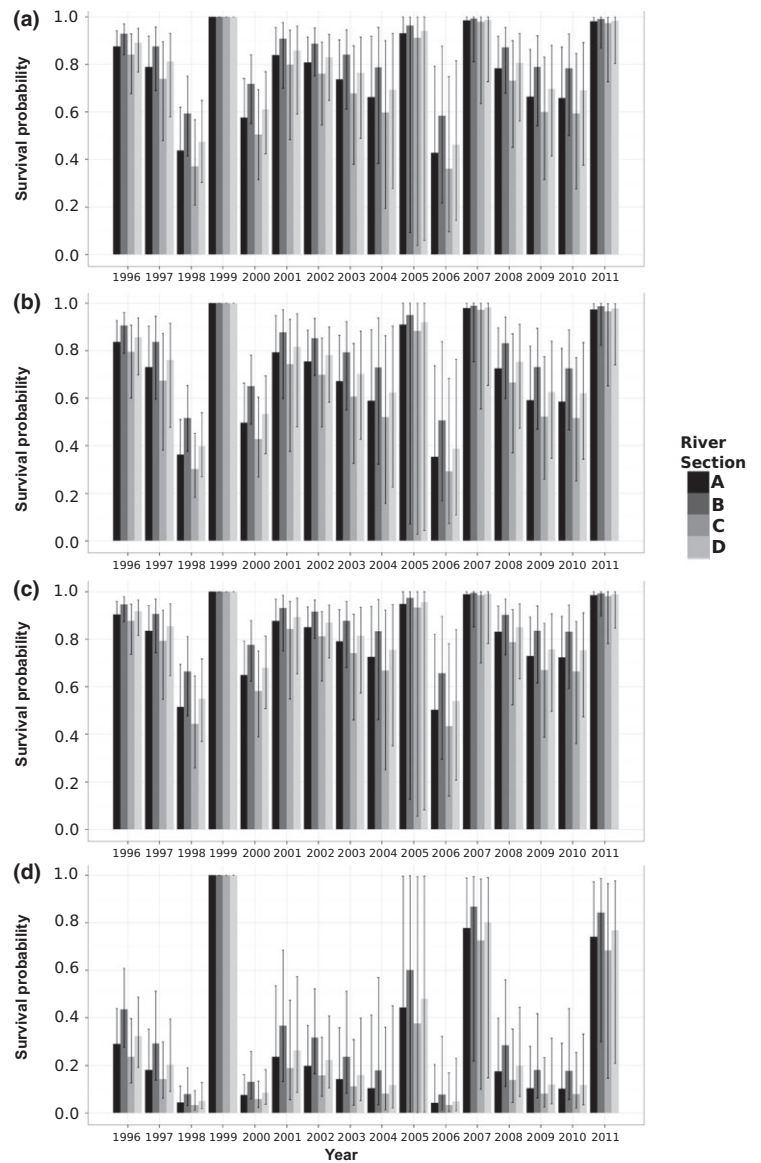


Fig. 4 Survival probabilities on each river section of the Frémur River (from the downstream river section A to the upstream river section D) of the three yellow eel stages (a) S_1 , (b) S_2 , (c) S_3 and silver eel stage (d) S_4 according to years. Error bars represent the 95% confidence interval.

barriers to upstream migrations (Feunteun *et al.*, 1998) are the most important determinant factors for density and size structure of the population (Feunteun *et al.*, 2003). In addition, eel growth, sex determination, and size/age at maturity usually co-vary with this spatial pattern (Krueger & Oliveira, 1999; Acou *et al.*, 2003; Feunteun *et al.*, 2003) because most of the environmental factors (salinity, productivity, etc.) are structured along the downstream–upstream gradient (Amoros & Petts, 1993). In the present study, survival probabilities did not seem to be affected by this gradient as no specific downstream–upstream pattern was observed. However, the presence of obstacles between each river section could explain this spatial variability. Indeed, as shown by Feunteun *et al.* (1998), the partition of the Frémur creates a partially enclosed envi-

ronment with specific characteristics (available food and space, and density of conspecifics). Furthermore, they demonstrated that most of the obstacles are impassable for eels that exceed 180–200 mm, and then even if the local conditions are unfavourable these eels could not migrate to other parts of the system, which could induce site-specific mortality. Temporal variation could have been caused by environmental effects; however, eels have high plasticity. Therefore, it is possible that in this temperate region, even very high water temperatures did not affect survival.

As highlighted in previous studies, density dependence could strongly regulate eel populations and may explain the survival variability (De Leo & Gatto, 1996; Vollestad & Jonsson, 1988; Lobón-Cerviá & Iglesias,

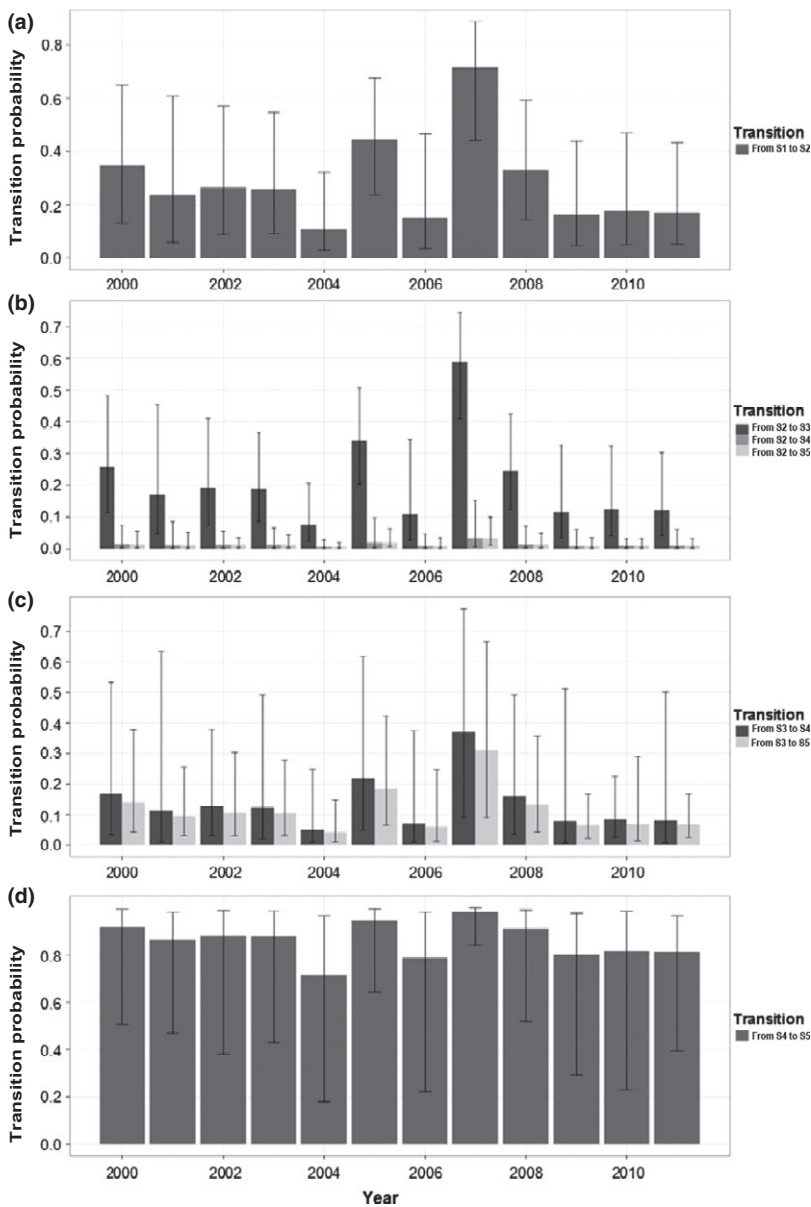


Fig. 5 Transition probabilities (error bars represent the 95% confidence interval) in the Oir River (a) from the yellow eel stage S_1 to S_2 , (b) from the yellow eel stage S_2 to S_3 , or to the silver eel stage S_4 or to the migratory silver eel stage S_5 , (c) from the yellow eel stage S_3 to the silver eel stage S_4 or to the migratory silver eel stage S_5 and (d) from the silver eel stage S_4 to the migratory silver eel stage S_5 over time.

2008; Bevacqua *et al.*, 2010). Furthermore, the negative feedback of the population size could be particularly important when populations approach their maximum size (Gaillard, Festa-Bianchet & Yoccoz, 1998; Eberhardt, 2002). Previous studies in the Frémur River, suggested that eel populations reach such a level in lotic habitats (Acou *et al.*, 2011). However, no significant relationship between eel density and survival was observed in the present study. This is unexpected as the Frémur should be saturated, and therefore increased density should lead to a decrease of survival. Non-mutually exclusive hypotheses could explain this discrepancy. Firstly, ignoring measurement error for density estimates may lead to an underestimation of the density-dependent relationship (Barker, Fletcher & Scofield, 2002; Carroll *et al.*,

2006). Secondly, the scale at which we studied density dependence could be inappropriate. As shown by various studies, density dependence is only meaningful if the study area is fine enough to capture the wide range of density of conspecifics experienced by the population in the study system and large enough to prevent individuals migrating in the search for food from unit to another during the studied year (Hassell, 1987; Stewart-Oaten, Murdoch & Walde, 1995; Ray & Hastings, 1996; Jenkins *et al.*, 1999). In the present study, we estimated density and survival at the scale of the river section. However, Ovidio *et al.* (2013) showed a longitudinal home range between 33 and 341 m in a small stream in Belgium. Therefore, to determine the effect of competition, we should have focused our study on density-

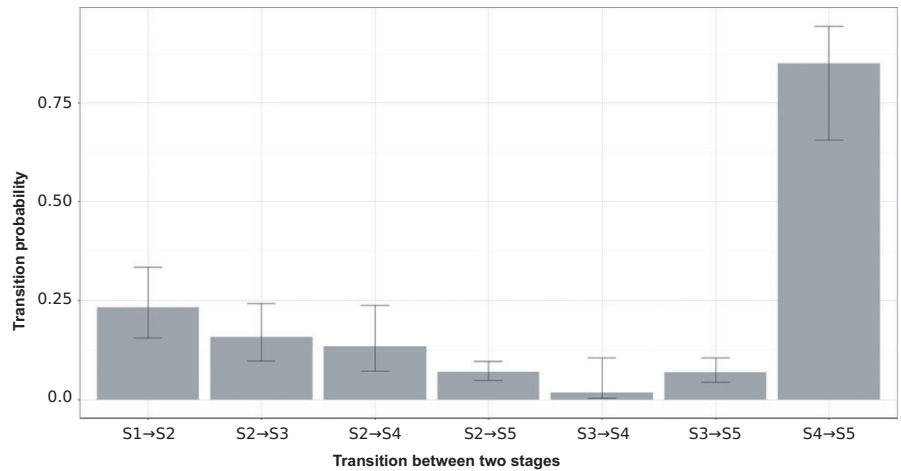


Fig. 6 Transition probabilities (error bars represent the 95% confidence interval) estimated in the Frémur River for the different eel life-stages.

Table 6 Statistics used to address the statistical support for the effect of covariates on the survival in the Frémur.

	Model statistical characteristics		ANODEV	
	Dev	AIC _c	Ftest _{cst/co/t}	Corrected P-value
Constant (F_{cst})	8109.5	8197.3		
Time	8045.7	8165.1		
Dependent (F_t)				
Covariate				
Models (F_{co})				
Dt	8107.9	8197.8	2.0	0.9
D1	8108.5	8198.4	1.3	0.7
D2	8095.8		21.6	1
D3	8108.8	8198.7	0.9	0.5
ND3	8106.7	8196.6	3.6	1
T_{mean}	8108.5	8199.4	1.6	0.8
Recruitment	8088.1	8194.8	14.2	1

dependent survival at an intermediate scale, between sampling sites (30–60 m) and river section (2–4 km). However, the use of this intermediate scale necessitates sufficient marked individuals in each specific area which was not the case in our study. Finally, our study focused on individuals with a size >150 mm representing >2-year-old individuals (Acou *et al.*, 2009). However, density-dependent processes in fish may decline with age (Cushing, 1975), so density-dependent processes on survival could only be applied to individuals smaller than those studied here. Some studies supported that density dependence is usually restricted to early life stages (Elliott, 1989; Persson & Greenberg, 1990; Dawson, 1991; Jenkins, Young & Davis, 1991). The important variability of recruitment, the instream density stability, and the absence of density dependence on survival of the

marked individuals (>150 mm) in the Frémur suggest that important density-dependent processes, especially on survival should be applied on the smallest individuals, i.e., the recruits (90–150 mm). However, to confirm this hypothesis, further studies are needed.

The important decrease in survival probabilities observed in the Frémur River in 1998, 2000, and 2006 are probably due to exceptional events than to the systematic effects of temperature or density. Despite no density-dependent effects on survival on our yellow eel stages, an exceptional recruitment may affect the survival of instream populations. According to a general hypothesis, density-dependent mortality caused by limited spatial resources, occurs when the colonisation of glass eels is sufficiently large and upstream migrants face an overcrowded river habitat (Moriarty, 1986; Vollestad & Jonsson, 1988; Feunteun *et al.*, 2003). Therefore, the low annual survival observed in 1998 in the resident population could be explained by the exceptional recruitment observed during this particular year. In 1998, recruitment was four times higher than the overall mean representing an increase of 0.36 eel m^{-2} in the whole system, effectively doubling the population. The large number of recruits observed this year might have induced intra- and inter-cohorts competition for resources and decreased survival of the recruits and the resident population (Feunteun *et al.*, 2003). However, in terms of biomass, the increase was more limited (increase of 1.1 g m^{-2} in the whole system). To confirm the potential correlation between the number of recruits and low survival more years with critical recruitments is necessary. Another event that may have played a role in explaining the annual decrease in eel survival is the draining of the Bois Joli reservoir that occurred between June 2006 and February 2007. The effect of this draining

	Model statistical characteristics		ANODEV		
	Dev	AIC _c	Ftest _{cst/co/t}	Corrected P-value	Deviance explained
Constant (F_{cst})	11115.9	11299.2			
On all yellow stages					
Time Dependent (F_t)	11096.8	11304.0			
Covariate Models (F_{co})					
Dt	11115.5	11301.1	0.2	1	
D1	11115.3	11300.1	0.4	1	
D2	11115.7	11301.3	0.1	0.9	
D3	11114.9	11300.5	0.6	1	
ND3	11114.4	11300.0	0.9	1	
T_{mean}	11115.5	11301.1	0.2	1	
On yellow stage S1					
Time Dependent (F_t)	1097.0	11304.0			
Covariate Models (F_{co})					
Dt	11115.9	11301.5	5.9E-06	0.05	4.2E-05
D1	11115.9	11301.5	9.8E-07	0.02	7.0E-06
D2	11115.8	11301.4	8.3E-05	0.2	
D3	11115.7	11301.3	0.0003	0.3	
ND3	11113.6	11299.2	0.003	1	
T_{mean}	11115.4	11301.2	0.0007	0.5	
On yellow stage S2					
Time Dependent (F_t)	11109.4	11316.3			
Covariate Models (F_{co})					
Dt	11115.6	11301.2	0.6	1	
D1	11115.6	11301.2	0.7	1	
D2	11115.7	11301.3	0.4	1	
D3	11115.1	11300.8	1.7	1	
ND3	11113.1	11298.7	10.5	1	
T_{mean}	11115.8	11301.4	0.2	1	
On yellow stage S3					
Time Dependent (F_t)	11104.1	11311.0			
Covariate Models (F_{co})					
Dt	11115.6	11301.2	0.3	1	
D1	11115.1	11300.7	1	1	
D2	11115.8	11301.4	0.1	1	
D3	11115.7	11301.3	0.2	1	
ND3	11115.7	11301.2	0.2	1	
T_{mean}	11110.7	11296.3	10.8	1	

Table 7 Statistics used to address the statistical support for the effect of covariates on the survival in the Oir River

on the eel population upstream is unknown; however, changes in the water level may have decreased food and habitat availability, and increased predation and migration, which could have led to the low eel survival in this year.

Unlike the Frémur River, annual survival probabilities observed were stable over time and space in the Oir River. Several hypotheses can be postulated. Firstly, upstream and downstream migrations are not disrupted by any obstacles, so when the local conditions are unfavourable for eels, individuals may move to another part of the system. Secondly, recruitment is remarkably lower and densities are fivefold lower than those of the Frémur, suggesting that the impact of density-dependent

processes on survival might slacken. Moreover, as in the Frémur River, the water temperatures should not affect survival. Finally, the contrasting survival observed in the two systems possibly result from differences in the characteristics of the two systems and the two sub-populations.

The contrasting pressures on those two sub-populations and their impact on annual survival and transition probabilities could lead to different life history strategies as suggested by the difference in sex ratio observed between the lotic habitats of the two rivers (predominantly females and males in the Oir and Frémur rivers respectively). The sexes of eels were hypothesised to develop and mature according to different life history

strategies, males using a time-minimising strategy and females using a size-maximising strategy which is consistent with our results (Helfman *et al.*, 1987; Vøllestad, 1992; Oliveira, 1999; Oliveira & McCleave, 2002). In the Oir River, annual survival probabilities increase with size classes but were constant in time and space. Therefore, the main advantage for eels in the Oir is to rapidly maximise their size (i.e., fecundity) to minimise mortality, thereby maximising their fitness. In the Frémur River, annual survival probabilities were slightly different between the yellow eel stages, but varied greatly within the study period. In this situation, the best strategy was to maintain sub-maximum growth rates to enhance survival and reach the minimum size necessary to achieve the spawning migration. Considering transition probabilities, it is likely that individuals from the Oir River continued to grow to reach the highest size at maturity and increased fecundity. On the contrary, eels from the Frémur River metamorphosed to the migratory silver phase at smaller sizes and younger ages and may have shifted resources away from somatic growth for gonadal development.

Finally, our results highlight that the extrinsic and/or intrinsic pressures on eel populations will determine the strategy developed by individuals to reach maturity. In the Frémur River, the time-minimising strategy of male eels that maintains sub-maximum growth rates to enhance survival, with limited variability between stages, to the size necessary to achieve a spawning migration, seems adapted to the system conditions (dams, high density, highly variable recruitment, etc.). On the contrary, in the system where the pressure is low and stable over time and space, a more risky strategy during the earlier years of an individual (survival lower in the younger stages) could be developed so they could enter a subsequent niche that achieve a higher fitness. If regulation processes exist at a size <150 mm in the Frémur and not in the Oir River, this could confirm that the determination of sex is strongly correlated with density pressure on young individuals (Krueger & Oliveira, 1999).

For conservation, demographic models were developed for assessing the escapement of silver eels (i.e., Arahamian *et al.*, 2007; Lambert & Rochard, 2007). However, such modelling over the whole life cycle is very complex and realistic demographic parameters such as survival rate need to be collated in different systems. Our study provides evidences that those models need to take into account size-specific survival but also a between-year variability in survival of >150 mm yellow eels to estimate reliable escapement of silver eels.

However, more studies are needed to understand the factors influencing survival variability.

Acknowledgements

This study was funded by the 'Region Bretagne', the MAVA Foundation, and 'Bretagne Grands Migrateurs'. The surveys and sampling were organised and operated by the company FISH PASS and the association 'Coeur Emeraude' in the Frémur River, and the INRA-Rennes and ONEMA in the Oir River. We are especially grateful to Frédéric Marchand (INRA), Julien Tremblay (INRA), Richard Delanoë (ONEMA), Virgile Mazel (FISH PASS), Sebastien Quinot (FISH PASS) and all the people that helped with sampling and data gathering. We are also grateful to ORE PFC for the salmonid data.

References

- 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., Gabriel G., Laffaille P. & Feunteun E. (2009) Differential Production and condition indices of premigrant eels in two small Atlantic coastal catchments of France. *American Fisheries Society Symposium*, **58**, 157–174.
- Acou A., Lefebvre F., Contournet P., Poizat G. & Crivelli A.J. (2003) Silvering of female eels (*Anguilla anguilla*) in two sub-populations of the Rhône delta. *Bulletin Français de la Pêche et de la Pisciculture*, **368**, 55–68.
- Acou A., Poizat G. & Crivelli A.-J. (2006) Errors in ocular index measurements in European eel *Anguilla anguilla* (L.). *Ecology of Freshwater Fish*, **15**, 578–582.
- Acou A., Rivot E., Van Gils J.A.N.A., Legault A., Ysnel F. & Feunteun E. (2011) Habitat carrying capacity is reached for the European eel in a small coastal catchment: evidence and implications for managing eel stocks. *Freshwater Biology*, **56**, 952–968.
- Amoros C. & Petts G.E. (1993) *Hydrosystèmes Fluviaux* (Eds C. Amoros & G.E. Petts). Masson, Paris.
- Angilletta M.J. Jr & Dunham A.E. (2003) The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. *The American Naturalist*, **162**, 332–342.
- Arahamian M.W., Walker A.M., Williams B., Bark A. & Knights B. (2007) On the application of models of European eel (*Anguilla anguilla*) production and escapement to the development of Eel Management Plans: the River Severn. *ICES Journal of Marine Science*, **64**, 1472–1482.
- Baglinière J.-L., Marchand F. & Vauclin V. (2005) Interannual changes in recruitment of the Atlantic salmon (*Salmo salar*) population in the River Oir (Lower Normandy, France):

- relationships with spawners and in-stream habitat. *ICES Journal of Marine Science*, **62**, 695–707.
- Baisez A. (2001) *Optimisation des suivis des indices d'abondances et des structures de taille de l'anguille européenne (Anguilla anguilla L.) dans un marais endigué de la côte atlantique?: relations espèce-habitat*. PhD Thesis, Toulouse 3 University, Toulouse.
- Barker R., Fletcher D. & Scofield P. (2002) Measuring density dependence in survival from mark-recapture data. *Journal of Applied Statistics*, **29**, 305–313.
- Bevacqua D., Andreollo M., Melià P., Vincenzi S., De Leo G.A. & Crivelli A.J. (2011) Density-dependent and inter-specific interactions affecting European eel settlement in freshwater habitats. *Hydrobiologia*, **671**, 259–265.
- Bevacqua D., Melià P., Leo G.A. & Gatto M. (2010) Intra-specific scaling of natural mortality in fish: the paradigmatic case of the European eel. *Oecologia*, **165**, 333–339.
- Bisgaard J. & Pedersen M.I. (1991) Mortality and growth of wild and introduced cultured eels (*Anguilla anguilla* (L.)) in a Danish stream, with special reference to a new tagging technique. *Dana*, **9**, 57–69.
- Bonhommeau S., Castonguay M., Rivot E., Sabatié R. & Le Pape O. (2010) The duration of migration of Atlantic *Anguilla* larvae. *Fish and Fisheries*, **11**, 289–306.
- Burnham K.P. & Anderson D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Science & Business Media, New York.
- Carle F.L. & Strub M.R. (1978) A new method for estimating population size from removal data. *Biometrics*, **34**, 621–630.
- Carroll R., Ruppert D., Stefanski L. & Crainiceanu C. (2006) *Measurement Error in Nonlinear Models: A Modern Perspective, Second Edition*. Chapman and Hall/CRC, New York.
- Caswell H. (2000) Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology*, **81**, 619–627.
- Choquet R., Lebreton J.-D., Gimenez O., Reboulet A.-M. & Pradel R. (2009a) U-CARE: utilities for performing goodness of fit tests and manipulating CAPTURE–RECAPTURE data. *Ecography*, **32**, 1071–1074.
- Choquet R., Rouan L. & Pradel R. (2009b) Program E-Surge: a software application for fitting multievent models. In: *Modeling Demographic Processes in Marked Populations* (Eds D.L. Thomson, E.G. Cooch & M.J. Conroy), pp. 845–865. Environmental and Ecological Statistics, Springer US, New York.
- Cucherousset J., Acou A., Blanchet S., Britton J.R., Beaumont W.R.C. & Gozlan R.E. (2011) Fitness consequences of individual specialisation in resource use and trophic morphology in European eels. *Oecologia*, **167**, 75–84.
- Cushing D.H. (1975) *Marine Ecology and Fisheries*. Cambridge University Press, Cambridge.
- Daverat F., Limburg K.E., Thibault I., Shiao J.-C., Dodson J.J. & Caron F., et al. (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.
- Dawson W.A. (1991) Otolith measurement as a method of identifying factors affecting first-year growth and stock separation of mackerel (*Scomber scombrus* L.). *ICES Journal of Marine Science*, **47**, 303–317.
- De Leo G. & Gatto M. (1996) Trends in vital rates of the European eel: evidence for density dependence? *Ecological Applications*, **6**, 1281–1294.
- De Leo G.A.D. & Gatto M. (1995) A size and age-structured model of the European eel (*Anguilla anguilla* L.). *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1351–1367.
- Dekker W. (2003) On the distribution of the European eel (*Anguilla anguilla*) and its fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 787–799.
- Drake J.M. (2005) Density-dependent demographic variation determines extinction rate of experimental populations. *PLoS Biology*, **3**, e222.
- Eberhardt L.L. (2002) A paradigm for population analysis of long-lived vertebrates. *Ecology*, **83**, 2841–2854.
- Elliott J.M. (1989) Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. I. The critical time for survival. *The Journal of Animal Ecology*, **58**, 987.
- 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., Laffaille P., Robinet T., Briand C., Baisez A. & Olivier J.-M., et al. (2003) A review of upstream migration and movements in inland waters by anguillid eels: toward a general theory. In: *Eel Biology* (Eds K. Aida, K. Tsukamoto & K. Yamauchi), pp. 191–213. Springer Japan, Tokyo.
- Gaillard J.-M., Festa-Bianchet M. & Yoccoz N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, **13**, 58–63.
- Grosbois V., Gimenez O., Gaillard J.-M., Pradel R., Barbraud C., Clobert J., et al. (2008) Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews*, **83**, 357–399.
- Hanski I., Foley P. & Hassell M. (1996) Random walks in a metapopulation: how much density dependence is necessary for long-term persistence? *Journal of Animal Ecology*, **65**, 274–282.
- Hassell M.P. (1987) Detecting regulation in patchily distributed animal populations. *Journal of Animal Ecology*, **56**, 705–713.
- Helfman G.S., Facey D.E., Hales L.S. & Bozeman E.L. (1987) Reproductive ecology of the American eel. In: *Common Strategies of Anadromous and Catadromous Fishes* (Eds M.J. Dadswell, R.J. Klauda, C.M. Moffitt, R.L. Saunders, R.A. Rulifson & J.E. Cooper), pp. 42–56. American Fisheries Society Symposium 1, Bethesda.

- Ibbotson A., Smith J., Scarlett P. & Aprhamian M. (2002) Colonisation of freshwater habitats by the European eel *Anguilla anguilla*. *Freshwater Biology*, **47**, 1696–1706.
- ICES (International Council for the Exploration of the Sea). 2013. Report of the Joint EIFAAC/ICES Working Group on Eels (WGEEL), 18–22 March 2013 in Sukarietta, Spain, 4–10 September 2013 in Copenhagen, Denmark. Gothenburg.
- Jacoby D. & Gollock M. (2014). *Anguilla anguilla*. *The IUCN Red List of Threatened Species*. Version 2014.2. [Online]. Available at: <http://www.iucnredlist.org/details/60344/0> [Accessed: 6 August 2014].
- Jenkins G.P., Young J.W. & Davis T.L.O. (1991) Density dependence of larval growth of a marine fish, the southern bluefin tuna, *Thunnus maccoyii*. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1358–1363.
- Jenkins T.M., Diehl S., Kratz K.W. & Cooper S.D. (1999) Effects of population density on individual growth of brown trout in streams. *Ecology*, **80**, 941–956.
- Josset Q., Trancart T., Mazel V., Charrier F., Frotté L., Acou A., et al. (2015) Pre-release processes influencing short-term mortality of glass eels in the French eel (*Anguilla anguilla*, Linnaeus 1758) stocking programme. *ICES Journal of Marine Science*, **73**, 150–157.
- Knights B. (2003) A review of the possible impacts of long-term oceanic and climate changes and fishing mortality on recruitment of anguillid eels of the Northern Hemisphere. *Science of the Total Environment*, **310**, 237–244.
- Krueger W.H. & Oliveira K. (1999) Evidence for environmental sex determination in the American eel, *Anguilla rostrata*. *Environmental Biology of Fishes*, **55**, 381–389.
- Laffaille P., Baisez A., Rigaud C. & Feunteun E. (2004) Habitat preferences of different European eel size classes in a reclaimed marsh: a contribution to species and ecosystem conservation. *Wetlands*, **24**, 642–651.
- Lambert P. & Rochard E. (2007) Identification of the inland population dynamics of the European eel using pattern-oriented modelling. *Ecological Modelling*, **206**, 166–178.
- Lasne E., Acou A., Vila-Gispert A. & Laffaille P. (2008) European eel distribution and body condition in a river floodplain: effect of longitudinal and lateral connectivity. *Ecology of Freshwater Fish*, **17**, 567–576.
- Lebreton J., Nichols J.D., Barker R.J., Pradel R. & Spende-low J.A. (2009) Modeling individual animal histories with multistate capture–recapture models. In: *Advances in Ecological Research* (Ed. H. Caswell), **41**, pp. 87–173. Academic Press, London.
- Lebreton J.-D., Burnham K.P., Clobert J. & Anderson D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.
- Lobón-Cervía J. & Iglesias T. (2008) Long-term numerical changes and regulation in a river stock of European eel *Anguilla anguilla*. *Freshwater Biology*, **53**, 1832–1844.
- Moriarty C. (1986) Variations in elver abundance at European catching stations from 1938 to 1985. *Vie et Milieu*, **36**, 233–235.
- Morin A., Lamoureux W. & Busnarda J. (1999) Empirical models predicting primary productivity from chlorophyll a and water temperature for stream periphyton and lake and ocean phytoplankton. *Journal of the North American Benthological Society*, **18**, 299–307.
- Naismith I.A. & Knights B. (1990) Modelling of unexploited and exploited populations of eels, *Anguilla anguilla* (L.), in the Thames Estuary. *Journal of Fish Biology*, **37**, 975–986.
- Noth E.G., Francis R.I.C.C. & Jellyman D.J. (2008) Factors influencing juvenile eel (*Anguilla* spp.) survival in lowland New Zealand streams. *New Zealand Journal of Marine and Freshwater Research*, **42**, 153–172.
- Oliveira K. (1999) Life history characteristics and strategies of the American eel, *Anguilla rostrata*. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 795–802.
- Oliveira K. & McCleave J.D. (2002) Sexually different growth histories of the American eel in four rivers in maine. *Transactions of the American Fisheries Society*, **131**, 203–211.
- Ovidio M., Serebinski A., Philippart J.-C. & Nzau Matondo B. (2013) A bit of quiet between the migrations: the resting life of the European eel during their freshwater growth phase in a small stream. *Aquatic Ecology*, **47**, 291–301.
- 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**, 127–140.
- Persson L. & Greenberg L.A. (1990) Interspecific and intraspecific size class competition affecting resource use and growth of perch, *Perca fluviatilis*. *Oikos*, **59**, 97.
- Pradel R., Wintrebert C.M.A. & Gimenez O. (2003) A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. *Biometrics*, **59**, 43–53.
- Prentice E.F., Flagg T.A. & McCutcheon C.S. (1990) Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. *American Fisheries Society Symposium*, **7**, 317–322.
- Ray C. & Hastings A. (1996) Density dependence: are we searching at the wrong spatial scale? *Journal of Animal Ecology*, **65**, 556–566.
- Rivot E., Prévost E., Cuzol A., Baglinière J.-L. & Parent E. (2008) Hierarchical Bayesian modelling with habitat and time covariates for estimating riverine fish population size by successive removal method. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 117–133.
- Sadler K. (1979) Effects of temperature on the growth and survival of the European eel, *Anguilla anguilla* L. *Journal of Fish Biology*, **15**, 499–507.
- Schulze T., Kahl U., Radke R.J. & Benndorf J. (2004) Consumption, abundance and habitat use of *Anguilla anguilla* in a mesotrophic reservoir. *Journal of Fish Biology*, **65**, 1543–1562.

- Sinclair A.R.E. & Pech R.P. (1996) Density dependence, stochasticity, compensation and predator regulation. *Oikos*, **75**, 164–173.
- Stewart-Oaten A., Murdoch W.W. & Walde S.J. (1995) Estimation of temporal variability in populations. *The American Naturalist*, **146**, 519–535.
- Tesch F.-W. (2003) *The Eel*. Blackwell Science, Oxford.
- Van Gils J.A., Edelaar P., Escudero G. & Piersma T. (2004) Carrying capacity models should not use fixed prey density thresholds: a plea for using more tools of behavioural ecology. *Oikos*, **104**, 197–204.
- Vøllestad L.A. (1992) Geographic variation in age and length at metamorphosis of maturing European eel: environmental effects and phenotypic plasticity. *Journal of Animal Ecology*, **61**, 41–48.
- Vøllestad L.A. & Jonsson B. (1988) A 13-year study of the population dynamics and growth of the European eel *Anguilla anguilla* in a Norwegian river: evidence for Density-dependent mortality, and development of a model for predicting yield. *Journal of Animal Ecology*, **57**, 983–997.
- Walsh C.T. & Pease B.C. (2002) The use of clove oil as an anaesthetic for the longfinned eel, *Anguilla reinhardtii* (Steindachner). *Aquaculture Research*, **33**, 627–635.
- Williams B.K., Nichols J.D. & Conroy M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, San Diego.

(Manuscript accepted 1 March 2016)