Differential Production and Condition Indices of Premigrant Eels in Two Small Atlantic Coastal Catchments of France

Anthony Acou
Équipe Recherche et Technologie (ERT) 52, Campus de Beaulieu, Bat. 25, 1er étage, Université de Rennes1, 35042, USA Rennes cedex, France

Gabriel Gaelle and Eric Feunteun
Laboratoire de Biologie et de l'Environnement Marin, Université de la Rochelle, Avenue Michel Crépeau, 17042, USA La Rochelle cedex 9, France

Pascal LaFfaille
Fish Pass, Bureau Expert Gestion Piscicole, 8 allée de Guerlédan, ZA Parc rocade sud, 35135, USA Chantepie, France.

Abstract.—This paper assesses potential production of premigrant European eels Anguilla anguilla based on analysis of sedentary eel populations in two small river systems in western France that are in close proximity. Abundance and biological characteristics were evaluated from electrofishing surveys conducted in three years in September and October, before the catadromous migration of silver eels. Mean density and biomass density of the eel population differed greatly between the systems (39 ± 6 ind.100 m ± 2 and 1352 ± 171 g.100 m ± 2 in the Frémur River and 3 ± 0.32 ind.100 m ± 2 and 385 ± 42 g.100 m ± 2 in the Oir River). Premigrants were dominated by males in the Frémur (85.8%) and by females in the Oir (79.0%). Estimated premigrant biomass density was 4.5-fold higher in the Frémur (254.5 g.100 m ± 2.year ± 1) than in the Oir (56.0 g.100 m ± 2.year ± 1). Mean Fulton's K condition factor was significantly higher for both sexes in the Oir (0.20 ± 0.004 and 0.20 ± 0.003 for males and females, respectively) than in the Frémur (0.17 ± 0.002 and 0.17 ± 0.004, respectively). The large differences in densities and biological characteristics of eels from neighboring catchments suggest that huge variability of both quantity and quality of silver eel production can be expected at the scale of the European stock.

Introduction

Anguillid eels support important commercial and recreational fisheries (McDowall 1990; Tesch 2003). According to Moriarty and Dekker (1997), 25,000 people earn income from the European eel *Anguilla anguilla*, whose fishery has a direct commercial value of 180 million Euro, plus 380 million Euro added value. However, since the 1980s, the European eel stock has declined substantially throughout its distribution range. The latter includes all accessible continental and coastal hydrosystems that link with the Baltic and North seas, as well as the Atlantic and Mediterranean coasts between Iceland and Morocco (Moriarty and Dekker 1997).

The International Council for the Exploration of the Sea (ICES; 1998) has recommended that all means should be taken to restore the depleted stock at all biological stages. In particular, it recommended increased escapement for glass eels, yellow eels, and silver eels and standard international escapement objectives (ICES 1998).

It is now generally agreed that despite uncertainties on the form of the stock-recruit relationship (i.e., the relationship between silver eel escapement from continental waters and subsequent glass eel recruitment back to continental waters), the best way to measure the effect of restoration efforts is to assess production, population structure (size, sex ratio, and age), and breeding potential of silver eels (Feunteun 2002).

In Europe, few quantitative data are available on the size of silver eel runs. Investigations in large water bodies typically use mark–recapture techniques (e.g., the Baltic Sea, Moriarty 1996; the Loire River, Boury et al., poster presented at the American Fisheries Society Annual Meeting 2003). In small river systems, exhaustive surveys have been conducted using wolf traps in a small number of rivers in northern Europe (e.g., the Frémur, Feunteun et al. 2000). However, silver eel escapement is unknown in most European water systems and a more efficient approach is needed to provide silver eel run estimates. In small coastal catchments, surveys are commonly conducted to characterize the status of the sedentary fraction of the eel stocks. Among sedentary eels, a proportion undergoes silvering metamorphosis before they start their downstream migration. Most premigrant eels achieve their silvering in late summer and then wait in the catchment until migration is triggered by environmental factors such as floods (Acou et al. 2000). By enumerating these premigrant eels, it is possible to estimate potential production of silver eels for a water course (Feunteun et al. 2000).

Robinet and Feunteun (2002) hypothesized that the probability that silver eels reach the spawning grounds and reproduce successfully varies among continental growing sites. A pan-European methodology to estimate the overall breeding potential of silver eels according to relevant criteria (fat composition, contamination by chemicals, parasitic load, etc.) is not yet ready for use because of the complexity in implementing such an approach. Use of silver eel condition indices may constitute a first step in this direction. Fulton's K condition factor has been demonstrated to indicate energy reserves of Atlantic salmon *Salmo salar* (Sutton et al. 2000), *Coregonus artedi* (Pangle and Sutton 2005), and *Gadus morhua* (Lambert and Dutil 1997; Grant and Brown 1999). Considering the importance of energy reserves during both transoceanic migration and reproduction of European eels (Boëtius and Boëtius 1980; Robinet and Feunteun 2002), we hypothesize that Fulton's K may represent a good index of silver eel breeding potential.

This paper estimates production of premigrant silver eels based on analysis of sedentary eel populations. To achieve this goal, we compared population characteristics of eel sub-populations in two coastal river systems of western France that vary substantially in the degree of human development. In order to assess the quality of silver eels produced in each catchment, we focused on sex ratio, mean weight, and Fulton's K condition factor in premigrant eels as indicators of reproduction potential in the two systems.

Methods

Study Sites

Catchment areas of the Frémur and Oir rivers are typical of the numerous river systems in western France. The Frému is a small river of northern Britanny, which discharges into the English Channel next to Saint Malo (Figure 1). Catchment area is approximately 60 km^2, and overall river and stream length is 46 km, with 17 km of main stream. Slope varies between 0.1% and 2%, with a mean of 0.6%. Tidal limit is at the Roche Good mill (Figure 1). The watershed contains two dams (Pont es Omnes and Bois Joli, Figure 1), which were impassable until the recent construction of fish lifts (Feunteun et al. 1998). The larger, at Bois Joli, is 14 m high and creates a 3×10^6 m^3 reservoir for drinking water. An eel lift for upstream migration was built in 1996. Impoundments formed by the two dams

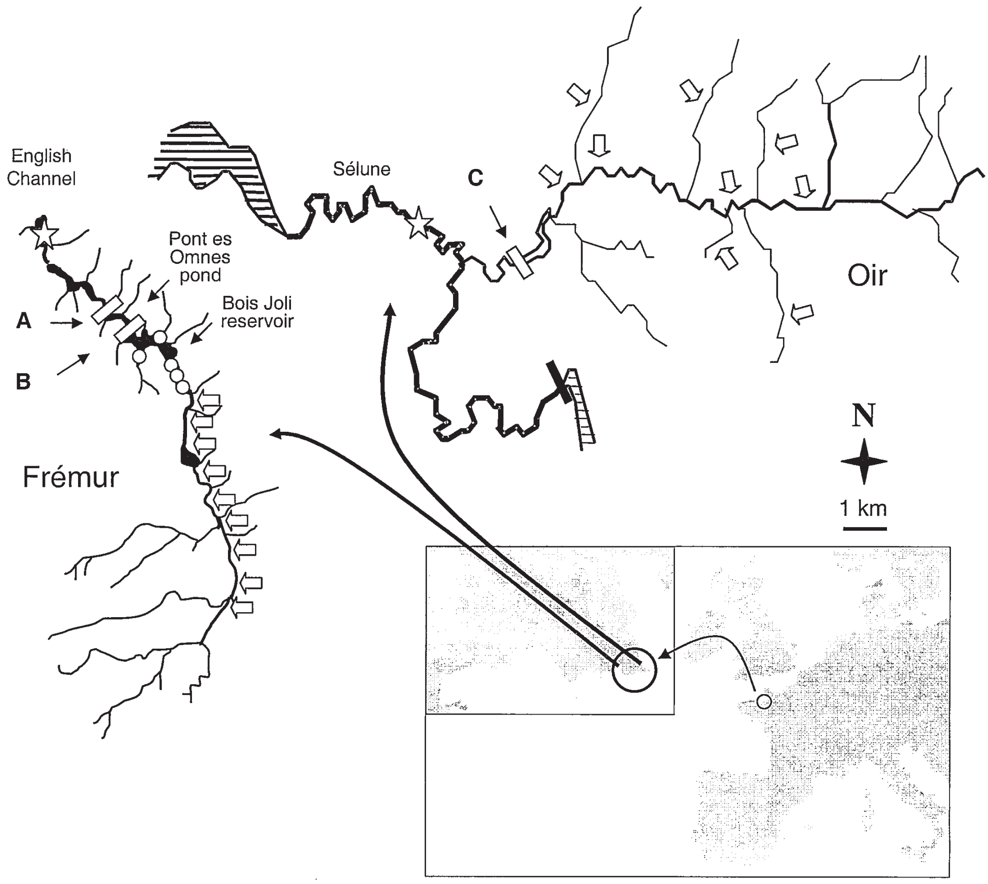

Figure 1. Location and characteristics of the Frémur and Oir catchments. Open arrows represent batches of two or three river sections sampled by electrofishing. Circles on the Frémur represent the locations of fyke-net fishing. Bars indicate the location of major dams. In the Frémur: A, Pont es Omnes dam (4.5 km from the sea) equipped with an eel-pass (designed to pass elvers) and a silver eel trap; B, Bois Joli dam (6 km from the sea) equipped with an eel-lift. In the Oir: C: Cerisel Mill (10 km from the sea). Stars represent tidal limits.

reduce velocity and increase depth, thereby creating aquatic communities dominated by lentic water species (bream *Abramis brama*, roach *Rutilus rutilus*, rudd *Scardinius erythrophtalmus*, tench *Tinca tinca*, northern pike *Esox lucius*, zander *Sander lucioperca*). 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 (Figure 1). Six minor works, including pipes under roads, water-flow gauging devices, and bridges, impose temporary obstacles to eel migration, depending on water level (Feunteun et al. 1998). Overall, the Frémur provides a wide range of habitats from high-velocity streams of the trout zone to lentic waters of the bream zone in downstream areas.

The Oir, a small river of southern Normandy, is a tributary of the Sélune that flows into Mont Saint-Michel-Bay (Figure 1). The centre of the Oir catchment is about 65 km east of the centre of the Frémur catchment. The Oir drains a 87-km^2 catchment, and overall length of the system is 120 km, including 25 km of main stem. Mean slope is 1.1%. Total wetted area upstream from Cerisel Mill (Figure 1), including the main stream and tributaries, is 22.9 ha. The Oir is obstructed by only one weir. The Oir is cool and not eutrophic and is one of the best rivers for brown trout *Salmo trutta* and Atlantic salmon in France.

Sedentary Stock Assessment

Sampling was conducted in the low-water-level period (September in the Frémur and October in the Oir), after the beginning of metamorphosis but before the migration of silver eels (Fontaine 1994). Sampling took place in both rivers in 2000, 2001, and 2002. Electrofishing was conducted with a Dream Electronic electrofisher set at DC 300 V and 3 A.

Frémur Sampling

Electrofishing was conducted in 30-m-long river sections delimited by 3-mm-mesh stop nets. A total of 29 river sections were sampled each year (Figure 1). These sections were located between 8.5 and 17 km from the sea. Mean width was 2.5 ± SD 0.5 m (range 0.7–4 m), and mean depth was 0.5 ± 0.1 m (range 0.15–1 m). These river sections covered about 2.3% of the overall stream length upstream of the Pont es Omnes dam (Figure 1). In Pont es Omnes pond and Bois Joli reservoir, eels were sampled with unbaited fyke nets with 6-mm mesh. Four sites were sampled with fyke nets in September 2000, three in September 2001, and two in September 2002.

Oir Sampling

A total of 32, 27, and 24 river sections that ranged between 100 and 1,000 m long were electrofished on the main stream and tributaries in October 2000, 2001, and 2002, respectively. These sections in the main stream were between 11.5 and 19.0 km from the sea. Sampling sections represented on average 8.0% of stream length upstream of Cerisel Mill (Figure 1). Mean width was 2.9 ± SD 1 m (range 0.6–4.5 m), and mean depth was 0.35 ± 0.14 m (range 0.05–0.47 m).

Migratory Potential Characteristics

Eels were anesthetized with 2-phenoxyethanol, measured (TL to the nearest mm) and weighed (W_t to the nearest g). Eels were allowed to recover in cool, well-oxygenated water for about 15 min before being returned to the water. No glass eels were found in either river. In this paper, elvers refers to pigmented eels less than 180 mm long. Most of these would be in their first year in continental waters. Silver eels were identified by three criteria (Feunteun et al. 2000): color of the back and belly, presence of a well-defined lateral line, and Ocular index (OI) greater than 6.5 according to Pankhurst's (1982) silvering threshold value. Oculuar index is the relation between TL and mean size of the two eyes, calculated as follows (Pankhurst 1982): OI = $25\pi/8$ TL $\{(A+B)^2_R+(A+B)^2_L\}$, where TL is total length, A and B are, respectively, the horizontal and vertical eye diameters, and R and L are right and left eyes. If only two of the criteria (most often the lateral line and the OI value) were met, the eel was designated as yellow/silver. Silver and yellow/silver eels are collectively referred to as premigrants. If only one (generally the OI value) or none occurred, the eel was recorded as yellow (Feunteun et al. 2000).

Sex was assigned by macroscopic observation of gonads, using the criteria described by Colombo et al. (1984), on subsamples of 75 and 35 silver eels caught in the Frémur and Oir catchments, respectively. In the Frémur, silver eels identified as male by this method ranged from 300 to 434 mm (N = 44; mean TL = 366 ± SE 4 mm), and silver eels identified as female ranged from 414 to 677 mm (N = 31; mean TL = 528 ± 10 mm). In the Oir, male silvers ranged between 334 and 437 mm (N = 13; mean TL = 373 ± 9 mm) and female silver eels ranged between 429 mm and 611 mm (N = 22; mean TL = 524 ± 11 mm). In both rivers, all silver eels greater than 440 mm were females, as has been shown in other studies (Rossi and Colombo 1979; Tesch 2003). In order to increase the number of sexed eels, all sampled premigrant eels (yellow/silver and silver eels) were classed as female if their length was greater than 440 mm and male if their length was less than or equal to 440 mm. All premigrant eels were assumed to be sexually differentiated. Sex ratio was expressed as proportion of females or males among premigrant eels. Fulton's K condition factor was calculated as $K = 100\times W_t/\text{TL}^3$ with W_t in g and TL in cm (Cone 1989).

Analysis

Premigrant characteristics.—In a previous study, Feunteun et al. (2000) observed no significant differences in length distribution between premigrant eels sampled in the Frémur catchment in September (electrofishing and fyke nets) and migrant eels captured the following season in the downstream trap at Pont es Omnes (Figure 1). This suggests that the sampling plan used in the Frémur provides reliable information about the silver eel population at the scale of the river system. In the present study, fyke-net results were not used for population estimates but were pooled with electrofishing results to describe the biological characteristics (W_t and K) of premigrant eels. Prior to statistical analysis and to respect normality of distribution, the data were log (x + 1) transformed. Factorial Anovas (with river (Frémur and Oir) and Year (2000, 2001, and 2002) as factors) were performed. Posthoc Tukey tests were used when Anovas were significant. χ^2 were used to test sex ratios and migratory potential proportions between years in each catchment. Length, weight, and K data presented are means ± SE.

Abundance Estimates

In both systems, total number and weight of fish in sections were assessed by the depletion method.

Frémur.—In all river sections, fish were removed after electrofishing passes. Most (92%) sessions consisted of two passes; the remainder had three passes. Total estimated eel numbers in each river section were calculated by the weighted maximum likelihood model of Carle and Strub (1978). Catchability was very high (on average 70% of the standing stock was caught at the first removal), as has been noted in previous studies (e.g., Lambert et al. 1994; Feunteun et al. 1998, 2000).

Oir.—Fishing sessions consisted of a single removal (C_1) or two-pass sessions (C_1 and C_2) termed "single" and "depletion" fishings, respectively. To estimate total number of eels in the Oir catchment, the model of Carle & Strub (1978) was used in 22 depletion sections. On average, 72% of the standing stock was caught at the first removal, suggesting similar catchabilities between the Oir and the Frémur. A linear regression was used to predict abundance estimated by Carle and Strub (1978) (C_{est}) from C_1 counts. The coefficient of determination (r^2) was tested by Anova. Slope and intercept of the linear regression were tested using a *t*-test. Independence between the residuals of the model and C_1 and normality of the residual distribution were tested using Pearson's correlation coefficient (*r*) and one-sample Kolmogorov Smirnov nonparametric test with Lillefor's option, respectively. The resulting relation was then used to assess total number of eels in both single and depletion sections according to C_1 removal.

In both systems, eel density and biomass density (expressed as ind.100 m^{-2} and g.100 m^{-2}) for each river section was calculated as total number and weight of estimated eels divided by area of the stream section. Eel density and biomass density are presented as means ± SE.

Stock assessment.—Stock for each catchment was estimated by multiplying mean density and biomass density by total wetted area. In the Oir, which has no ponds, total wetted area was 22.9 ha. In the Frémur, most (91.15%) wetted area is ponds and reservoirs where no measurement of population densities are available. Extrapolation of stream densities to the overall surface of pond/reservoir habitats would lead to biased estimates, since this method would ignore eel microhabitat selection (Broad et al. 2001). In a study on spatial organization of eels in the Frémur, Laffaille et al. (2003) found that large eels tend to be in intermediate-to-high depths with intermediate abundance of vegetation. In Pont es Omnes pond and Bois Joli reservoir, only a narrow shoreline strip (ca. 2.5 m wide) provides such habitats for both small and large eels. Jellyman and Chisnall (1999) for *A. australis* and Schulze et al. (2004) for *A. anguilla* confirmed that eels are mainly confined to shorelines because of the availability of cover (e.g., rocks or macrophytes) and presence of food. The 2.5-m shoreline strip of Pont es Omnes pond and Bois Joli reservoir amounted to 2.1 ha. Thus, total wetted area used for stock-assessment calculations in the Frémur was 7.4 ha (2.1 ha for pond/reservoir habitat and 5.3 ha for running portions).

Feunteun et al. (2000) extrapolated from density estimates to the whole stream surface and analyzed mark–recapture records of PIT-tagged silver eels to assess eel population size in the Frémur catchment. Size of the silver eel stock in the basin was calculated from size of the total silver eel run (trap data) and the fraction of the tagged population recaptured in the run (recapture), using the Lincoln-Petersen method. The two methods produced similar estimates of the numbers of silver eels (3000 silver eels on average in 1996 and 1997), suggesting that both approaches are reliable (Feunteun et al. 2000).

Results

Population structure

Frémur.—Eels captured by electrofishing and fyke netting ranged in length from 56 to 774 mm (Figure 2). Modal length of young eels ranged from 160 to 180 mm between 2000 and 2002. Proportions of elvers (eels < 180 mm) were equivalent in 2000 and 2002 (26.0% and 27.7% of total catch, respectively) but were significantly higher in 2001, with 42.0% of the total catch (χ^2 = 3215.72, df = 2, $p < 0.001$). For all years combined, 85.1% of premigrant eels belonged to the 300-to-440-mm size-class and were assumed to be males. Proportions of males among premigrants were 80.3% in 2000, 87.5% in 2001, and 89.5% in 2002, 85.8% for all years pooled.

Oir.—Eels captured by electrofishing ranged between 117 mm and 682 mm (). Length structures of each biological stage (yellow, yellow/silver, and silver) were not statistically different among years (Kolmogorov-Smirnov test, $p > 0.1$), suggesting a steady population over time. Proportion of young eels less than 180 mm represented only 1.1% (N = 8) of captures in all years. Premigrant population structure was dominated by females (i.e., eels > 440 mm) in all years (85.7% in 2000, 70.0% in 2001, 81.2% in 2002, 79.0% for all years pooled).

Premigrant characteristics.—Mean weight of premigrant males was 83 ± SE 2.0 g (range 41–167) in the Frémur and 120 ± 5.5 g (range 79–156) in the Oir. Mean K of premigrant males was 0.172 ± 0.002 (range 0.095–0.231) in the Frémur and 0.197 ± 0.003 (range 0.170–0.217) in the Oir. Mean weight of premigrant females was 256 ± 18.0 g (range 161–541) in the Frémur and 290 ± 11.6 g (range 156–547) in the Oir. Mean K of premigrant females was 0.168 ± 0.004 (range 0.136–0.204) in the Frémur and 0.196 ± 0.003 (range 0.141–0.247) in the Oir. For both sexes, eels were significantly heavier in the Oir than in the Frémur (Table 1; Figure 4). Similarly, Fulton's K condition factor was significantly higher in the Oir than in the Frémur for both sexes (Table 1; Figure 5).

Abundance

Frémur.—Total mean density and biomass density for all stages during the three study years were high, with 39 ± SE 6 ind.100 m^{-2} and 1,353 ± 171 g.100 m^{-2}, respectively (Table 2). Proportion of silver eels was similar in 2000 (5.9%) and 2002 (5.8%) but was significantly lower in 2001 (1.3%) (Anova: factor = Year, df = 2, F = 8.77, $p < 0.001$). The proportion of yellow/silver eels varied between 0.1% in 2002 and 3.2% in 2001. Thus, yellow/silver eels and silver eels constituted a migratory potential of 8.3% in 2000, 4.5% in 2001, and 5.9% in 2002. Mean biomass density of the population decreased from 1,752 ± SE 400 g.100 m^{-2} in 2000–1,126 ± 238 g.100 m^{-2} in 2001 and 1,180 ± 203 g.100 m^{-2} in 2002. Premigrant biomass density dropped significantly from 420 g.100 m^{-2} in 2000–172 ± 9 g.100 m^{-2} in 2001 and 2002 (Table 2).

Oir.—A linear regression between C_{est} and C_1 was performed in the Oir catchment ($C_{est} = 1.17 \pm 0.13 \times C_1 + 1.1 \pm 0.52$, $r^2 = 0.80$, F = 79.9, $P < 0.001$) with significant slope and intercept (t-Test, $P < 0.05$). No significant correlation between residuals and C_1 was observed (r = 0.0, P = 1). Abundances of the first removal were log-transformed, since residual distribution did not meet the normality assumption (Kolmogorov-Smirnov test, d = 0.31, $P < 0.05$). Estimated mean total density and biomass density were

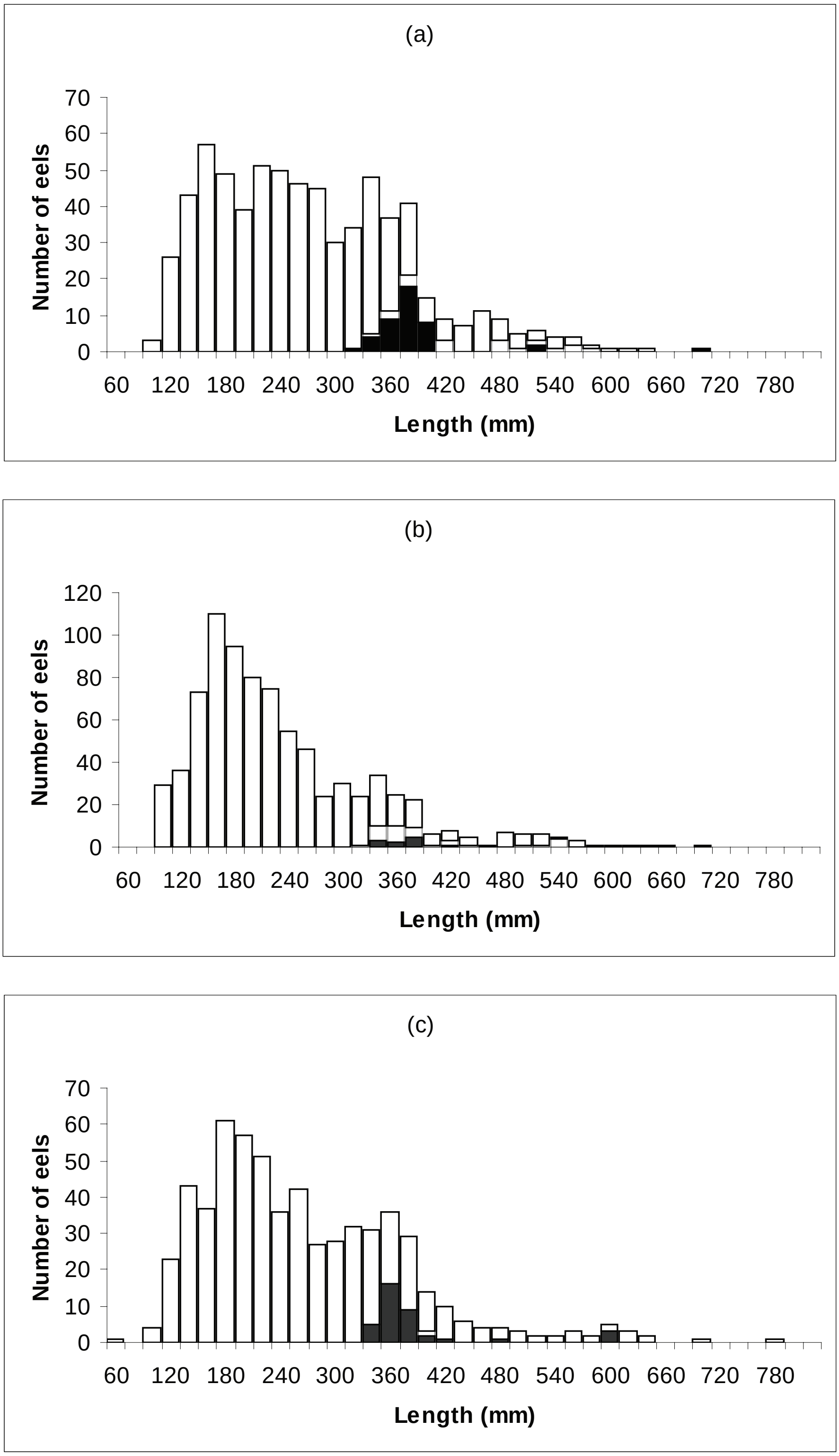

Figure 2. Length histogram of eels sampled by electrofishing and by fyke net in the Frémur catchment in September (a) 2000, (b) 2001 and (c) 2002. Open bars, yellow eels (N = 614 in 2000, N = 770 in 2001 and N = 562 in 2002); solid bars, silver eels (N = 43 in 2000, N = 11 in 2001 and N = 37 in 2002); hatched bars, yellow/silver eels (N = 9 in 2000, N = 30 in 2001 and N = 1 in 2002).

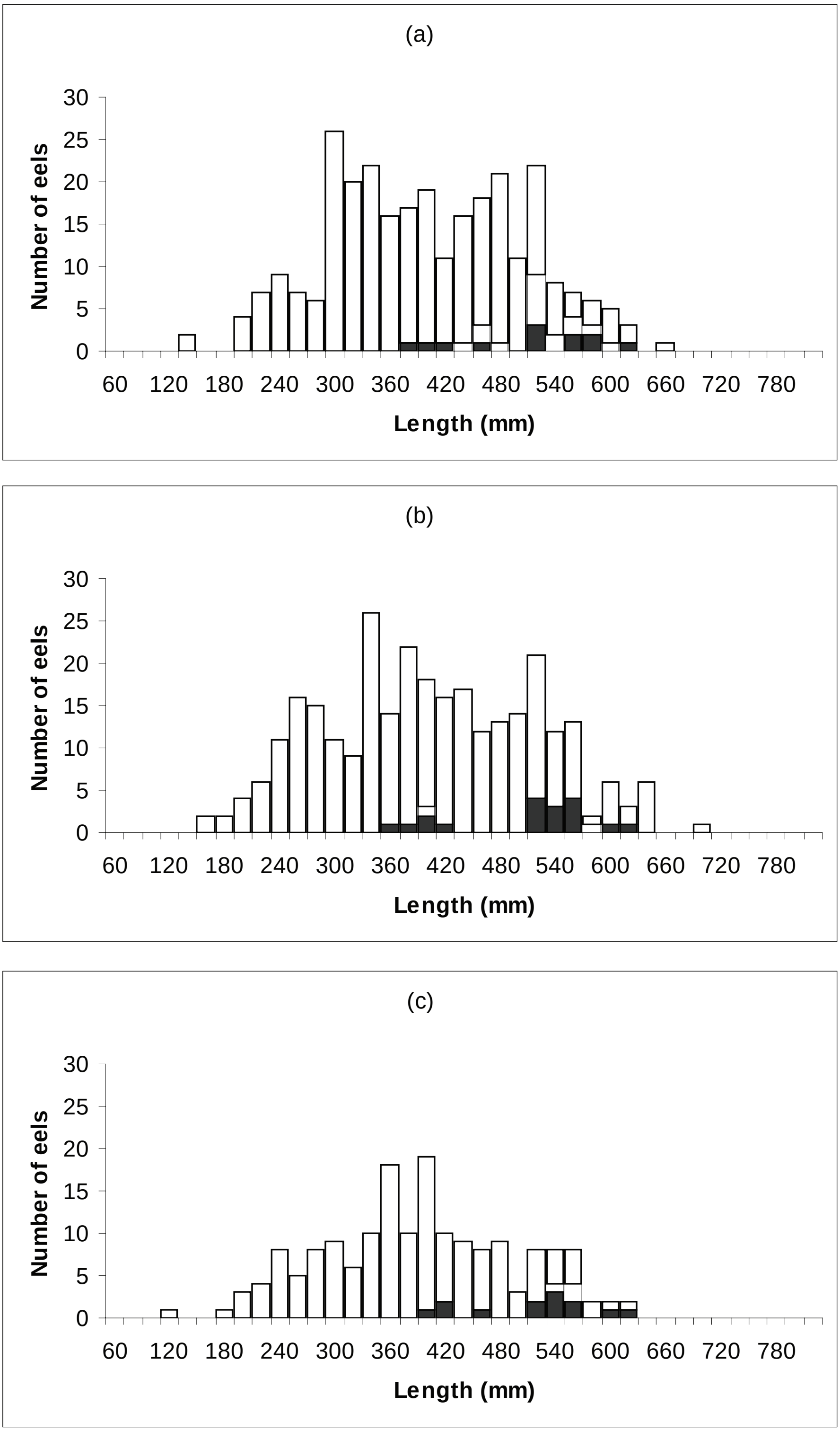

Figure 3. Length histogram of eels sampled by electrofishing in the Oir catchment in October (a) 2000, (b) 2001 and (c) 2002. Open bars, yellow eels (N = 256 in 2000, N = 272 in 2001 and N = 155 in 2002); solid bars, silver eels (N = 12 in 2000, N = 8 in 2001 and N = 13 in 2002); hatched bars, yellow/silver eels (N = 16 in 2000, N = 2 in 2001 and N = 3 in 2002).

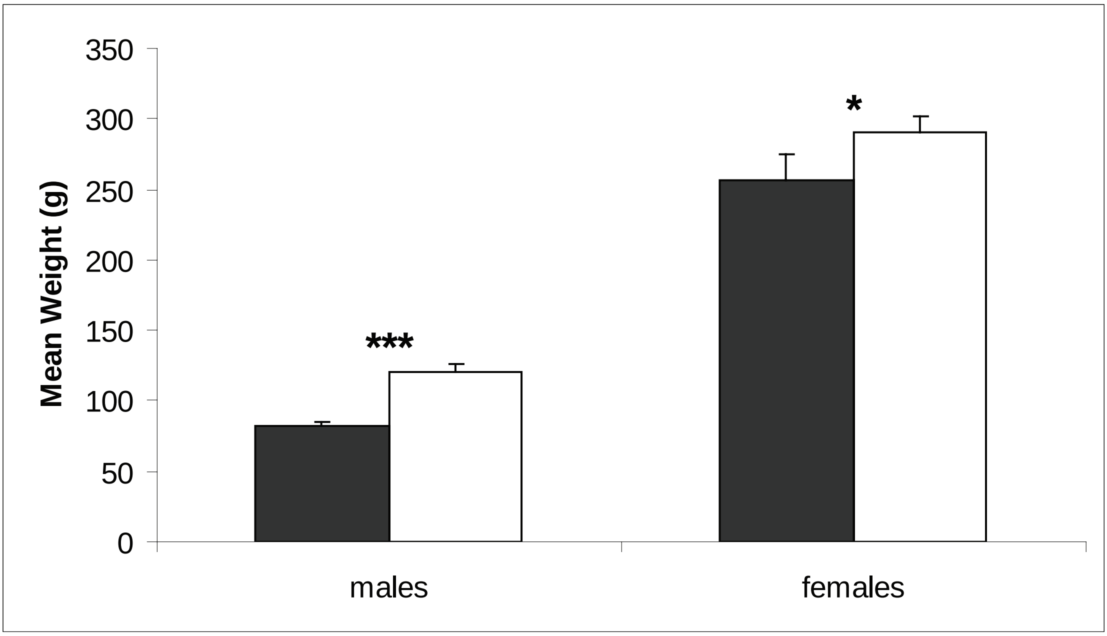

Figure 4. Mean weight (±SE) of potential migrants (yellow/silver and silver eels) for both sexes by river. Solid bars, eels caught in the Frémur R.; open bars, eels caught in the Oir R. Significance of Tukey's posthoc comparison test is shown as * = $P < 0.05$, ** * = $P < 0.001$.

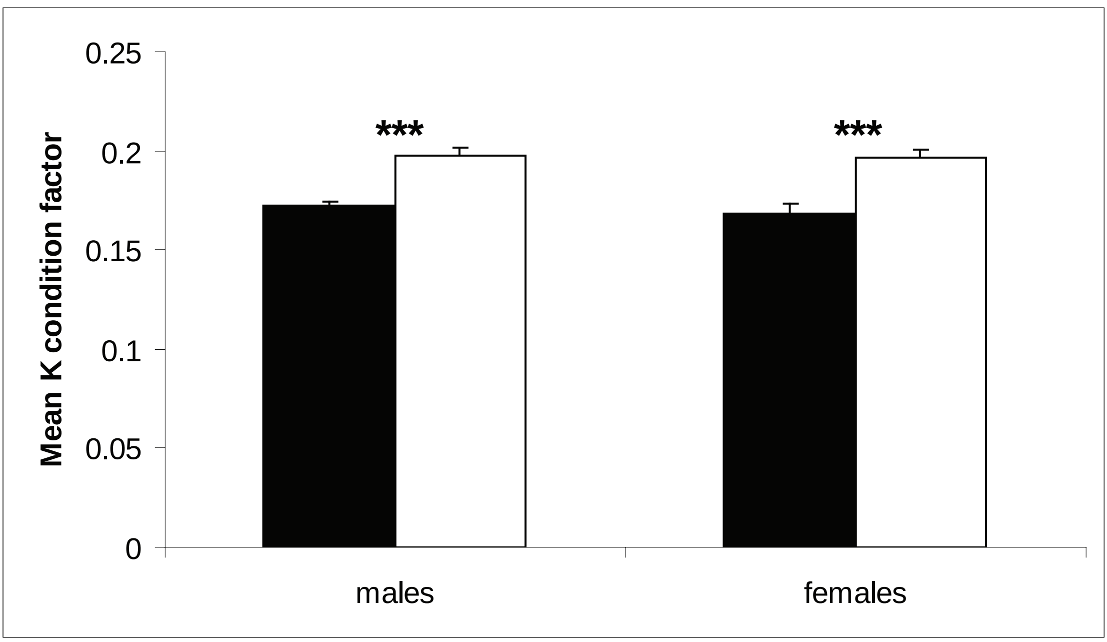

Figure 5. Mean Fulton's K condition factor (±SE) of premigrant (yellow/silver and silver) eels for both sexes by river. Solid bars, eels caught in the Frémur R.; open bars, eels caught in the Oir R. Significance of Tukey's posthoc comparison test is shown as * = $P < 0.05$, ** * = $P < 0.001$.

Table 1. Anova results for the effect of independent variables (Year, River and Year × River) on Weight and K of male and female pre-migrant eels (only significant interactions are shown).

	Effect	Sum of Squares	d.f.	Mean Square	F	P
Male pre-migrants						
Weight						
	River	18621.46	1	18621.46	46.16	0.00
	Year	2273.80	2	1136.90	2.81	0.06
	Error	50420.50	125	403.36		
K						
	River	0.76	1	0.76	11.92	0.00
	Year	0.10	2	0.05	0.81	0.45
	Error	8.00	125	0.06		
Female pre-migrants						
Weight						
	River	31320.47	1	31320.47	4.39	0.04
	Year	9544.36	2	4772.18	0.67	0.51
	Error	477489.02	67	7126.70		
K						
	River	1.15	1	1.15	20.99	0.00
	Year	0.11	2	0.05	0.98	0.38
	Error	3.66	67	0.05		

approximately 13- and fourfold lower than in the Frémur, amounting to 3 ± SE 0.32 ind.100 m^{-2} and 385 ± 42 g.100 m^{-2}, respectively (Table 3). During the study period, proportion of silver eels varied from 3.1% of the whole stock in 2000–8.2% in 2002, but this variability was not statistically significant (Anova, df = 2, F = 1.65, P = 0.19). Yellow/silver proportions declined significantly from 3.0% in 2000–0.1% in 2001 of the overall resident eels (Anova, df = 2, F = 3.85, $P < 0.05$). Therefore, the proportion of premigrant eels amounted to 6.2% in 2000, 5.4% in 2001, and 8.7% in 2002. Premigrant eel biomass density was stable in time with 48 g.100 m^{-2} in 2000, 51 g.100 m^{-2} in 2001, and 69 g.100 m^{-2} in 2002 (Anova, df = 2, F = 0.15, P = 0.86).

Premigrant Estimates

The population of premigrant eels in the Frémur was estimated to be 2,475 eels (315 kg) in 2000, 1,500 (124 kg) in 2001, and 1,448 (134 kg) in 2002 (Table 2). For the Oir, the premigrant population was estimated as 412 eels (110 kg) in 2000, 412 (117 kg) in 2001, and 595 (159 kg) in 2002 (Table 3). Thus, estimated premigrant populations in the Frémur were approximately fourfold higher than those of the Oir in each year. Estimated Frémur premigrant eel biomass was approximately 1.5-fold higher than that of the Oir during the study period.

However, because of the contrast in sex ratio between rivers, the number of female premigrants was greater in the Oir than in the Frémur (mean population 378 ± SE 57 in the Oir and 286 ± SE 103 in the Frémur) (Table 4). Moreover, because of the larger size of the females in the Oir, the biomass of female premigrants was substantially greater in the Oir (103 ± SE 14 kg.$year^{-1}$) than in the Frémur (31 ± 15 kg.$year^{-1}$) (Table 4).

Table 2. Characteristics of the sedentary fraction of the eel population from 2000 to 2002 estimated by electrofishing in the Frémur River. Stock is the population size in the whole catchment in numbers and in kilograms, estimated as the product of mean density and area of streams + a 2.5 m wide strip on the perimeter of impoundments. N is the number of sampled stations.

	All stage	Yellow eels	Pre-migrant eels		
			Yellow/silver eels	Silver eels	Total
2000 (N = 29)					
Density (ind.100 m-2)					
Mean	39.71	36.41	0.96	2.34	3.30
SE	9.19	8.69	0.28	0.68	0.73
Stock (no.)	29783	27309	716	1758	2475
Biomass (g.100 m-2)					
Mean	1751.82	1332.08	155.37	264.37	419.74
SE	402.49	325.84	59.93	95.97	118.37
Stock (kg)	1314	999	117	198	315
2001 (N = 29)					
Density (ind.100 m-2)					
Mean	44.54	42.55	1.41	0.59	2.00
SE	13.43	13.08	0.45	0.29	0.65
Stock (no.)	33407	31910	1058	439	1500
Biomass (g.100 m-2)					
Mean	1125.84	960.52	118.53	46.78	165.31
SE	238.00	202.60	40.15	23.58	53.27
Stock (kg)	844	720	89	35	124
2002 (N = 29)					
Density (ind.100 m-2)					
Mean	32.75	30.82	0.04	1.89	1.93
SE	7.75	7.42	0.04	0.67	0.70
Stock (no.)	24566	23118	31	1417	1448
Biomass (g.100m-2)					
Mean	1179.96	1001.44	4.71	173.82	178.53
SE	203.86	158.28	4.71	58.39	60.55
Stock (kg)	885	751	4	130	134

Discussion

Numerous studies based on life history traits (population structure, growth pattern, age at silvering) emphasize that the watershed is the relevant ecological unit to assess silver eel biomass (e.g., Feunteun et al. 2000; Acou et al. 2003). The present investigation of silver eel production in two small Atlantic catchments supports this conclusion.

In the Frémur, estimated densities were 39 ± SE 6 ind.100 m^{-2} and 1,352 ± 171 g.100 m^{-2}. These values are very high compared with other west European catchments (Moriarty and Dekker 1997; Feunteun et al. 1998). For example, Carrs et al. (1999) reported that 71% of density estimates at 1,462 sites in English rivers and streams were more than 5 ind.100 m^{-2}. Vollestad and Jonsson (1988) estimated eel density at

Table 3. Characteristics of the sedentary fraction of the eel population from 2000 to 2002 estimated by electrofishing in the Oir. Stock is the population size in the whole catchment in numbers and in kilograms, estimated as the product of mean density and area of streams. N is the number of sampled stations.

	All stage	Yellow eels	Pre-migrant eels		
			Yellow/silver eels	Silver eels	Total
2000 (N = 32)					
Density (ind.100 m-2)					
Mean	2.89	2.71	0.09	0.09	0.18
SE	0.44	0.45	0.03	0.05	0.06
Stock (no.)	6610	6206	200	205	412
Biomass (g.100 m-2)					
Mean	342.72	294.80	24.28	23.63	47.91
SE	45.16	42.76	10.13	12.99	16.96
Stock (kg)	785	675	56	54	110
2001 (N = 27)					
Density (ind.100 m-2)					
Mean	3.35	3.17	0.00	0.17	0.18
SE	0.51	0.51	0.00	0.06	0.06
Stock (no.)	7671	7270	11	397	412
Biomass (g.100 m-2)					
Mean	455.37	404.43	1.19	49.75	50.94
SE	83.47	84.26	1.01	21.79	21.89
Stock (kg)	1043	926	3	114	117
2002 (N = 24)					
Density (ind.100 m-2)					
Mean	2.97	2.70	0.02	0.24	0.26
SE	0.17	0.73	0.01	0.09	0.10
Stock (no.)	6793	6190	44	559	595
Biomass (g.100 m-2)					
Mean	356.59	287.34	5.85	63.40	69.25
SE	95.50	87.49	3.78	22.59	23.85
Stock (kg)	817	658	13	145	159

1.16 ind.100 m^{-2} in the Imsa River (Norway), based on the total estimated population size in the catchment divided by the total area of water (including the deeper parts of lakes). Some of the highest density estimates (50–1300 ind.100 m^{-2}) were observed in Danish streams (Rasmussen 1983), including mostly elvers (< 150 mm). In Frémur samples, proportions of elvers (< 180 mm) varied between 26% and 42% during the study period, suggesting interannual variability of recruitment, which was also observed in an eel-pass survey (Figure 1; Acou, unpublished data). However, we suggest that the shortness of the Frémur, its good location for glass eels ar-

Table 4. Estimated production of male and female pre-migrant (yellow/silver and silver) eels in number (no.) and biomass (kg) in the Frémur and Oir catchments.

	Frémur				Oir			
	2000	2001	2002	Mean ± SE	2000	2001	2002	Mean ± SE
Male pre-migrants								
Production (no.)	1987	1281	1296	1521 ± 233	51	124	111	95 ± 23
Production (kg)	253	106	120	160 ± 47	14	35	30	26 ± 6
Female pre-migrants								
Production (no.)	488	219	152	286 ± 103	361	288	484	378 ± 57

rivals, and the restoration of upstream migration by means of the eel lifts could explain this high abundance (see Feunteun et al. 2000). Moreover, fishing pressure was quite low (no commercial fishery), and anglers focused mainly on cyprinids, esocids, and percids. Lastly, we did not observe predation mortalities, since piscivorous birds (including cormorants and ardeids) were scarce in the study area.

In the Oir River, elvers (eels < 180 mm) represented only 1.1% of the total catch during the sampling period. It seems that colonization of the Oir by young recruits is low. Distance from the sea is the most important structuring parameter for abundance and mean size of European eels (Ibbotson et al. 2002). In the present study, distances of electrofishing sampling sections from the sea did not differ greatly between the Frémur (8.5–17 km) and the Oir catchments (11.5–19 km). It seems unlikely that the small difference in distance from the sea (3 km) could explain the large difference in elver proportions in the Frémur (40.0%) and the Oir (1.1%). Configuration of the Oir River could explain part of this variability. The Oir is a small tributary of the main river (Sélune) and flows into the Sélune 8 km from the sea. The Oir discharge was 10-fold lower than that of the Sélune (1258 ± SD 364 $l.s^{-1}$ and 12213 ± 3898 $l.s^{-1}$, respectively; INRA, unpublished data) between March and July 1999. Water-flow attraction is crucial for the orientation of glass eels and elvers during their freshwater migration (Legault 1994). We suggest that eel recruitment in the Sélune is higher than in the Oir, as confirmed by sampling in the Sélune (A. Acou, unpublished data). The Frémur, unlike the Oir, recruits all freshwater-seeking eels in its estuary. Thus, global densities (in number and biomass) observed in the Oir were approximately 13- and fourfold weaker (3.07 ± SE 0.32 ind.100 m^{-2} and 385 ± 42 g.100 m^{-2}, respectively) than in the Frémur.

Premigrant fractions are dominated by males (85.8%) in the Frémur and by females (79.0%) in the Oir. Female dominance is commonly found in headwater streams where densities are low (Parsons et al. 1977). Helfman et al. (1987) proposed that female eels have an extended larval period and dominate in northern latitudes due to differential larval distribution. The high variation in sex ratio between the neighboring Frémur and Oir catchments does not support the hypothesis that latitude is a determining factor of sex ratio. Instead, our results are consistent with Krueger and Oliveira's (1999) view that density influences eel sex ratios, with high densities promoting the production of males. However, other factors, such as trophic composition of the aquatic ecosystem, may also influence sex determination.

For both sexes, potential migrants in the Oir had significantly higher mean weight and condition factor than those of the Frémur. Lipid, protein, and energy content in fish are positively related to body condition (Lambert and Dutil 1997; Grant and Brown 1999; Sutton et al. 2000; Pangle and Sutton 2005). Fish with a lower condition index may have encountered poor feeding conditions or parasitic infections (Lambert and Dutil 1997; Yaragina and Marshall 2000).

Kangur and Kangur (1998) found that eels in the shallow, eutrophic Lake Vortsjarv in Estonia showed a strong linear relationship ($r = 0.81$, $P < 0.0001$) between condition factor and biomass of invertebrates (i.e., *Chironomus plumosus*), the main trophic resource of the lake. Nutrition condition could vary between the Frémur and the Oir according to (1) food availability, (2) food quality, (3) turnover of food, and (4) intra- and interspecific competition. The high eel density in the Frémur may lead to intensified intraspecific competition in this river. Moreover, because of eutrophication, strong cyanotoxin blooms (especially Microcystin-LR) are regularly observed in the Pont es Omnes pond and Bois Joli reservoir in late summer (L. Brient, University of Rennes, personal communication). We recently analyzed levels of Microcystin-LR in fresh liver of 30 migrant silver eels caught in winter at the Pont es Omnes downstream trap (Figure 1; A. Acou, unpublished data). Results showed that 50% of them are contaminated with a mean toxin level of 28.1 ± SD 22.4 ng.g^{-1}. Microcystin-LR has been found to induce severe liver damage and growth inhibition in fish (Rahberg et al. 1991; Kent et al. 1994; Tencalla et al. 1994). In the Oir, eel densities are low and cyanobacteria blooms are not observed. Hence differences in feeding opportunities, as mediated by intraspecific competition and cyanotoxin exposure, may contribute to the differences between the two systems in mean weight and condition factor. Further comparative studies between the rivers are needed to clarify these effects.

At the silver stage, the eel stops feeding and must have large lipid reserves to sustain gonad development during the long migration back to the Sargasso Sea (Boëtius and Boëtius 1980). Based on condition factors, it appears that the probability of reaching the spawning grounds in the Sargasso Sea is higher for silver eels reared in the Oir catchment than in the Frémur catchment.

Premigrant biomass densities in the Frémur and Oir are at the upper and median ranges, respectively, of silver eel biomass densities in European standing waters. For example, in the Imsa River (Norway), a mean silver eel biomass density of 22.7 g.100 m^{-2} was reported between 1975 and 1987 (Vollestad and Jonsson 1988). In salt or brackish Italian lagoons, silver eel biomass density varied between 65 g.100 m^{-2} and 190 g.100 m^{-2} (Rossi 1979; Rossi and Cannas 1984). In our study, estimated premigrant biomass density was 4.5-fold higher in the Frémur (254.5 g.100 m^{-2}) than in the Oir (56 g.100 m^{-2}). However, female premigrant biomass densities were equivalent in the two systems (43 g.100 m^{-2} and 45 g.100 m^{-2}, respectively).

We realize that our results constitute an approximation of silver eel production and that further validation is needed to generalize our methods for small catchments. Schulze et al. (2004) found that eels in a pond concentrated in shallow waters near the shoreline, although some were in deeper water farther from shore. In the Frémur, because density estimates were not available for the impoundments, we assumed that eels in this habitat were limited to a 2.5-m-wide peripheral strip, with density similar to that measured by electrofishing in streams. Under this assumption, eels would be absent from 95% of the Frémur's wetted area. If this assumption is incorrect, our estimates of eel density would nevertheless be roughly valid for running water. Failure of the assumption would have greater consequences on estimates of total stock. If impoundment waters farther than 2.5 m from shore contain eels, even at low densities, the total stock could be much larger than the one estimated in the present study (Table 4). Mean yearly estimated production of premigrant eels in the Frémur River (1,521 ± 233 premigrant males and 286 ± 103 premigrant females; Table 4) may therefore constitute an underestimation of total production

Our estimates of silver eel production assume a one-to-one relation between premigrant (yellow/silver and silver) eels and escapement of silver eels in the subsequent fall. However, the time required for an eel to complete its silvering process remains unclear (Cottrill et al. 2002). Failure of this assumption could lead to biased estimates of production. To clarify this point, we have begun a study using PIT tags to assess recapture rates of externally identified yellow/silver and silver eels.

To our knowledge, this study is the first to associate quantitative estimates of the number of premigrant eels that will undergo a catadromous migration with data on the quality of migration candidates (i.e., body condition). Even if our method needs further validation, we showed that silver eel production and mean Fulton's K condition factor vary between two small river systems (wetted areas < 60 ha) that are in close proximity. European eel stocks exist in small and fragmented subpopulations (Dekker 2000). If rivers that are only 65 km apart show this degree of variability, we can expect a very high level of variation in production ha^{-1} and quality of silver eels across the species' range. Contribution of silver eels by water system is the main component of the current conservation strategy. However, we believe that the question of quality of animals among river systems, which is presumed to influence reproductive success on the spawning grounds, is also a key issue that must be urgently pursued for European eel conservation.

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