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Decline of North Atlantic eels: a fatal synergy?

Thierry Wirth[1,2*] **and Louis Bernatchez**[1]

[1]*Québec-Océan, Département de Biologie, Université Laval, Ste-Foy, Québec G1K 7P4, Canada*
[2]*Max-Planck Institut für Infektionsbiologie, Department of Molecular Biology, Schumannstrasse 21/22, 10117 Berlin, Germany*

Panmictic species pose particular problems for conservation because their welfare can be addressed effectively only on a global scale. We recently documented by means of microsatellite analysis that the European eel (*Anguilla anguilla*) is not panmictic but instead shows genetic isolation by distance. In this study, we extended the analysis to the American eel (*A. rostrata*) by applying identical analytical procedures and statistical power. Results obtained for the American eel were in sharp contrast with those obtained for the European eel: the null hypothesis of panmixia could not be rejected, and no isolation by distance was detected. This implies that the species must be managed as a single population. Using Bayesian statistics, we also found that the effective population sizes for both species were surprisingly low and that the populations had undergone severe contractions, most probably during the Wisconsinan glaciation. The apparent sensitivity of eels to climatic changes affecting the strength and position of the Gulf Stream 20 000 years ago is particularly worrying, given the effects of the ongoing global warming on the North Atlantic climate. Moreover, additional short-term stresses such as surging glass eel prizes, overfishing and lethal parasitic infections negatively affect eel population size. The fascinating transatlantic migration and life cycle of Atlantic eels is also their Achilles' heel as these negative short- and long-term effects will probably culminate in a fatal synergy if drastic conservation measures are not implemented to protect these international biological resources.

Keywords: conservation; Atlantic eels; Bayesian inference; microsatellites; demographic history; climatic changes

1. INTRODUCTION

Understanding fluctuations in marine fish stocks is important, as changes in population size appear to show a significant relationship with climatic and oceanographic variability. The North Atlantic Oscillation (NAO) correlates with marine fish assemblages (Attrill & Power 2002) while the decline of production of young North Sea cod (*Gadus morhua*) appears to be correlated with a warming of the North Sea over the past 10 years (O'Brien *et al.* 2000). Moreover, NAO-driven marine fish and zooplankton abundance has affected fulmar population dynamics (Thompson & Ollason 2001). North Atlantic eels have a basin-wide distribution, are nearly panmictic and are expected to be even more affected by North Atlantic climatic changes than most marine species as the relative strength and position of the Gulf Stream is vital for their dispersal and successful migration. *Anguilla anguilla* and *A. rostrata* are therefore ideal candidates for tracking ongoing and past effects of climatic change.

The natural history and reproductive migration to the Sargasso Sea of North Atlantic eels have fascinated mankind for millennia. Aside from their general migration pattern, little is actually known about the oceanic phase of their reproductive cycle, or their effective population sizes, demography and oceanic movements (Schmidt 1925; Tesch 1977). A better knowledge of eel biology is essential as the abundances of both European (*A. anguilla*) and American (*A. rostrata*) eels have steadily declined since the early 1980s. The annual catch of the European eel has decreased by more than 40% from 1988 to 1998 according to the United Nations Food and Agriculture Organization, and a major decline in recruitment in the St Lawrence River basin has been observed for *A. rostrata* (Castonguay *et al.* 1994*a*; Haro *et al.* 2000; International Council for the Exploration of the Sea (ICES) 2001).

Population genetics offers an efficient means to acquire the essential knowledge needed for a global management of Atlantic eel populations. Moreover, these two species form the foundation for the panmixia paradigm (Avise *et al.* 1986; Lintas *et al.* 1998), although this hypothesis was rejected by patterns of isolation by distance and genetic structure recently reported in the European eel (Daemen *et al.* 2001; Wirth & Bernatchez 2001; Maes & Volckaert 2002). Here, a combination of genetic information gathered from highly polymorphic microsatellite loci and Bayesian statistics is used to test the null hypothesis of random mating in the American eel, as well as to investigate the population demography and effective population size (the size of an ideal population that best predicts changes in genetic diversity such as inbreeding coefficients or variance in allelic frequencies) of both Atlantic eel species. Finally, we discuss the putative correlation between demographic patterns for the species and climatic change.

2. MATERIAL AND METHODS

(a) *Sampling and DNA extraction*

A total of 402 *A. rostrata* were collected from eight different rivers between Florida and the St Lawrence River during spring and autumn 1999, covering a distance of over 3000 km (figure 1).

* Author for correspondence (wirth_t@mpiib-berlin.mpg.de).

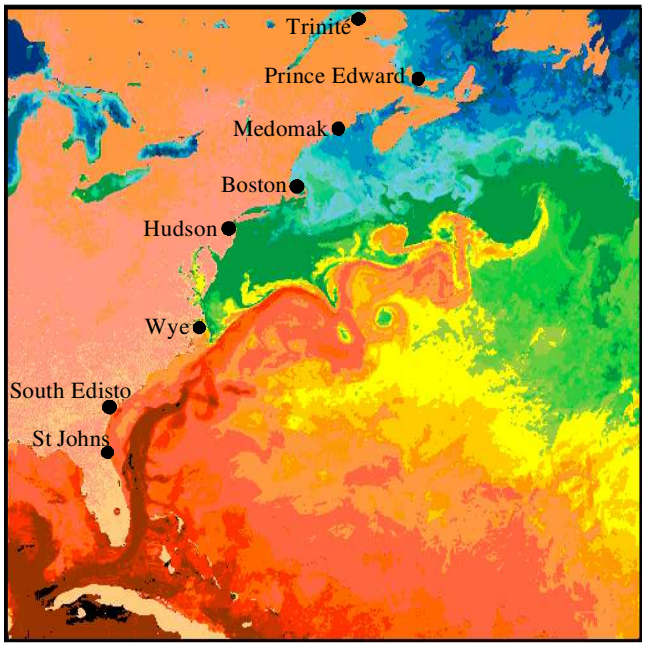

Figure 1. Sampling locations. Petite rivière de la Trinité ($n = 52$), Prince Edward Island ($n = 50$), Medomak River ($n = 50$), Boston Harbour ($n = 50$), Hudson River ($n = 50$), Wye River ($n = 50$), South Edisto River ($n = 50$) and St Johns River ($n = 50$). All samples consisted of yellow eel fin clips with the exception of the Boston Harbour samples where glass eels were collected. Samples were collected from spring to autumn 1999. This image is a thermal infrared sea surface temperatures (SST) image showing the clockwise Gulf Stream (NASA source). Colours represent thermal data and range from 2–9 °C (dark blue) to 24–28 °C (red and orange).

This study also includes 611 *A. anguilla* individuals collected at 13 locations covering the entire distribution of the European eel (Wirth & Bernatchez 2001). Glass eels or fins were stored in 95% ethanol until DNA extraction was performed according to standard methods (Maniatis *et al.* 1982).

(b) *Genotyping*

Quantification of genetic variation was performed using seven microsatellite loci specifically developed for *A. rostrata* and *A. anguilla* (*Aro054*, *Aro063*, *Aro095*, *Aro121*, *Ang101*, *Ang114* and *Ang151*). The microsatellite flanking sequences and primers are available on GenBank under the accession numbers AF237896–AF237902. Polymerase chain reactions (PCRs) were performed in duplex or triplex with polymerase and rhodamine-marked primers (Perkin–Elmer) as outlined in Wirth & Bernatchez (2001). Amplifications were conducted in a 10 µl volume with 10–50 ng of DNA, 300 pmol of each primer, 75 µM of each nucleotide, 1.2 mM of $MgCl_2$, 1 × Taq buffer (10 mM of Tris–HCl pH 9, 50 mM of KCl) and 0.25 units of *Taq* polymerase (Perkin–Elmer). The PCR protocol comprised an initial denaturation at 95 °C for 4 min, 32 cycles of denaturation at 95 °C for 30 s, primer annealing at 55 °C for 45 s and extension at 72 °C for 1 min, and a final 5 min extension at 72 °C. A volume of 2 µl of each PCR product was mixed with 2 µl of blue formamide containing 10% of GS350 internal size standard, carboxytetramethylrhodamine (TAMRA 350 bp) and loaded onto a 5% polyacrylamide gel for a 2.25 h electrophoresis at 3000 V using an ABI377 automated DNA sequencer (Perkin–Elmer, Foster City, CA). The fragment sizes were determined by reference to a size standard run in each lane using the software GENSCAN v. 2.1 and GENOTYPER v. 2.0 (Perkin–Elmer).

(c) *Genetic variability and population genetics parameters*

Allelic diversity, genetic variation (observed heterozygosity under Hardy–Weinberg equilibrium (HWE)), deviation from HWE and genetic differentiation were calculated with GENEPOP v. 3.1 (Raymond & Rousset 1995). Variation in allelic frequencies among samples was assessed first by testing the null hypothesis of homogeneity in allelic distribution by Fisher's exact test using the Markov chain method. The standardized variance in allelic frequencies was used as an estimator of F_{ST} (Weir & Cockerham 1984) as implemented in GENETIX v. 4.02 (Belkhir *et al.* 2000).

(d) *Isolation by distance*

The relationship of genetic divergence to geographical separation of sites was examined by measuring the Cavalli-Sforza chord distance (D_{CE}) on the basis of allelic frequencies across the seven loci between each pair of samples (Cavalli-Sforza & Edwards 1967). The significance of the relationship between D_{CE} and geographical distance cannot be evaluated using standard regression techniques, as the regression is based on non-independent pairwise comparisons. We used Mantel's test (Mantel 1967) to assess the significance of the observed correlations using GENETIX v. 4.02.

(e) *Phylogenetic inference*

Cavalli-Sforza and Edwards' chord distance was used to construct a phylogenetic tree using a neighbour-joining algorithm (Saitou & Nei 1987). Support for the tree nodes was assessed by bootstrapping over loci (5000 iterations). The tree was built using PHYLIP v. 3.6 (Felsenstein 1993) from raw allelic frequencies.

(f) *Coalescence and demographic parameters using Bayesian statistics*

This approach (Beaumont 1999) assumes a stepwise mutation model and estimates the posterior probability distributions of the genealogical and demographic parameters of a sample using Markov chain Monte Carlo simulations based on microsatellite data. The estimated parameters are scaled in terms of current population size and two main demographic parameters are quantified: (i) t_f, which is a measure of time in generations, is defined as t_a/N_0, where t_a denotes the number of generations that have elapsed since the decline or expansion began, and (ii) r, which is defined as N_0/N_1, where N_0 is the current effective number of chromosomes ($2N_e$) and N_1 is the number of chromosomes at some previous point in time t_f. For a declining population $r < 1$, for a stable population $r = 1$ and for expanding populations $r > 1$. The procedure also estimates θ, which is defined as $2N_0\mu$, where μ is the mutation rate (mutation locus^{-1} generation^{-1}). The analyses were performed assuming exponential demographic change for both species. Owing to a restriction of the model, which assumes that there are no more than 2000 coalescent and mutational events in the genealogy, we used the algorithm sinf.exe provided in Beaumont's package in order to produce subsample files of 100 individuals from our complete dataset. Three different chains were run for each analysis to confirm the convergence of the results. In the analysis, rectangular priors of the log parameter values have been used. The limits for N_0, N_1, μ and t_f were taken to be 10^3–10^6,

Table 1. Summary statistics for American and European eels.
(The estimates of N_0, N_1, r and t_a were calculated based on a mutation rate of 5×10^{-4} per generation (Angers & Bernatchez 1998). Abbreviation: MRCA, most recent common ancestor.)

	mean	s.d.	median	0.025 quantile	0.975 quantile
Anguilla rostrata ($n = 100$)					
log (r)	−1.818	0.086	−1.819	−1.990	−1.657
log (t_f)	−0.453	0.033	−0.454	−0.524	−0.388
log (θ)	0.953	0.101	0.949	0.776	1.180
number of mutations	1505	197	1535	1087	1784
MRCA	81.133	28.543	75.828	41.121	144.270
N_0	9236	2228	8882	5964	15 146
N_1	605 820	133 882	604 108	387 222	876 072
r	0.015	0.003	0.015	0.010	0.022
t_a	3250	754	3124	2078	5132
A. anguilla, Atlantic Ocean ($n = 100$)					
log (r)	−2.050	0.148	−2.066	−2.303	−1.726
log (t_f)	−0.336	0.035	−0.337	−0.407	−0.271
log (θ)	0.620	0.146	0.606	0.351	0.905
number of mutations	1382	272	1449	828	1764
MRCA	174.617	72.457	173.019	54.028	338.606
N_0	4410	1544	4034	2242	8028
N_1	484 363	128 080	471 746	255 532	776 508
r	0.009	0.004	0.009	0.005	0.019
t_a	2030	694	1840	1038	3602
A. anguilla, Mediterranean Sea ($n = 100$)					
log (r)	−1.985	0.197	−2.029	−2.257	−1.516
log (t_f)	−0.533	0.038	−0.532	−0.608	−0.462
log (θ)	0.692	0.178	0.665	0.414	1.082
number of mutations	1476	207	1476	1006	1787
MRCA	171.305	73.066	163.075	60.395	320.200
N_0	5388	2542	4620	2592	12 084
N_1	496 678	154 366	470 966	273 780	888 778
r	0.011	0.006	0.009	0.006	0.030
t_a	1562	680	1376	766	3408
A. anguilla, Baltic and North Seas ($n = 100$)					
log (r)	−1.926	0.110	−1.925	−2.142	−1.701
log (t_f)	−0.385	0.041	−0.384	−0.469	−0.308
log (θ)	0.636	0.130	0.652	0.323	0.857
number of mutations	1161	221	1157	743	1644
MRCA	121.171	51.961	113.120	54.524	271.172
N_0	4514	1266	4486	2100	7190
N_1	380 612	108 210	370 958	194 946	620 760
r	0.012	0.003	0.012	0.007	0.020
t_a	1856	506	1838	950	2924

10^3–10^7, 10^{-3}–10^{-4} and 10^{-3}–10, respectively. We found that the method converged appropriately for both single-locus and multilocus data and supported a model of population decline for both the European and the American eels. We decided to present only the multilocus data in the present report.

3. RESULTS AND DISCUSSION

(a) *Genetic diversity and population genetic structure*

American eels from eight different locations were genotyped at the same seven Mendelian-inherited microsatellite loci used in our previous study (Wirth & Bernatchez 2001) on *A. anguilla*. All loci were highly polymorphic, with the average number of alleles per locus (per sample, ± s.e.) ranging from 14.4 (± 2.00) to 27.1 (± 3.3). Observed and expected mean heterozygosities per sample ranged from 0.79 (± 0.05) and 0.85 (± 0.02) to 0.91 (± 0.05) and 0.95 (± 0.01), respectively. Probability tests of HWE using a Markov chain approach (Raymond & Rousset 1995) showed significant departures from HWE in three out of 56 cases after Bonferroni (Rice 1989) corrections ($\alpha = 0.05$, $k = 8$), a number similar to that expected by chance alone ($0.05 \times 56 = 2.8$).

(b) *Panmixia in the American eel*

Genetic differentiation based on allelic frequency distribution, as well as the very low fixation index value ($F_{ST} = 0.0022$, $p < 0.01$) over all samples, were significant ($p = 0.0020$; 10 000 iterations). This value is smaller than

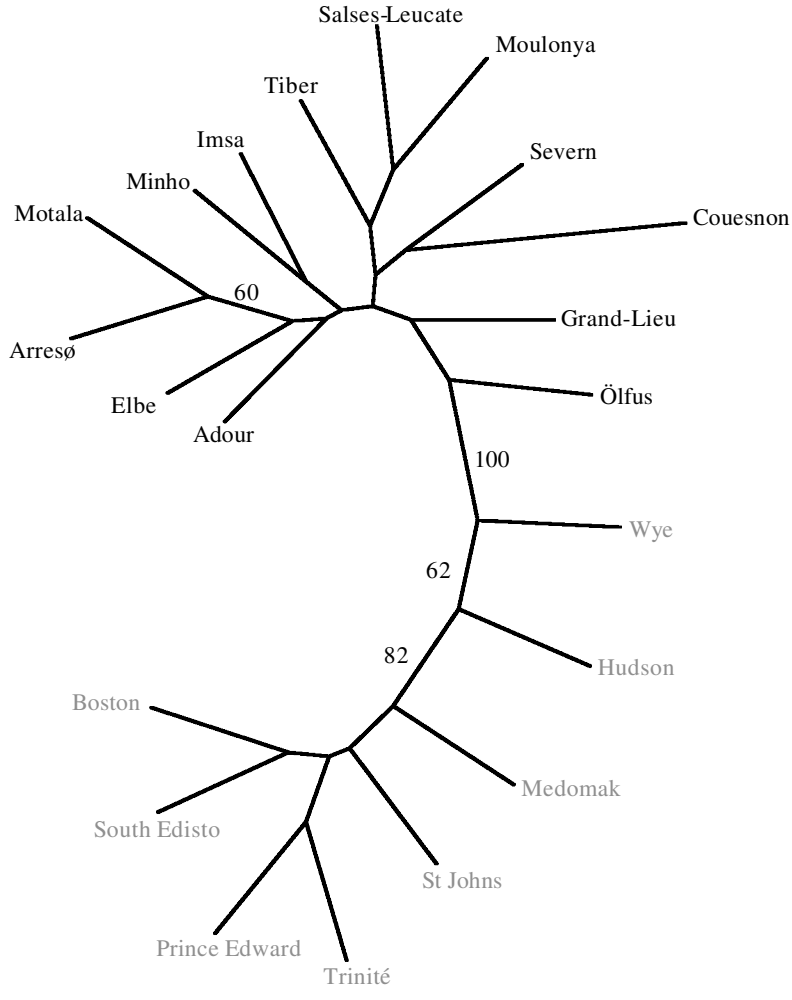

Figure 2. Bootstrapped neighbour-joining tree of Cavalli-Sforza and Edward's chord distances among eight American eel samples (grey lettering) and 13 European eel samples. The tree was constructed using GENDIST, NEIGHBOR and CONSENSE programs in PHYLIP v. 3.6 (Felsenstein 1993) and visualized with TREEVIEW (Page 1996). Values on the nodes are the percentage of bootstrap replicates over loci that are greater than 50 ($n = 1000$).

could be generated by sampling error alone (Waples 1998) ($\times$ average sample size $1/2 = 0.01$). Furthermore, no evidence for population structuring was revealed by plotting pairwise D_{CE} values (Cavalli-Sforza & Edwards 1967) against coastal distances. The Pearson's correlation (Mantel 1967) r between the two factors was not significant and close to zero ($r = 0.003$, $p = 0.496$). This result is in sharp contrast with the highly significant pattern of isolation by distance reported for the European eel. However, as more samples were used in our previous study, we checked for the possible effect of type II error. Thus, eight *A. anguilla* populations from the total of 13 were randomly selected 100 times, and the Mantel test was applied to assess the significance of the observed correlations. All Pearson's correlations (r) between genetic and geographical distances were positive (mean = 0.454, range of 0.188–0.624) and two orders of magnitude larger than for the American eel samples. Moreover, 91 out of the 100 resamplings were significant at the 0.10 level (mean = 0.0475, and range of p-values = 0.002–0.289). Therefore, the absence of isolation by distance in *A. rostrata* is unlikely to be the result of small sample size, and, consequently, panmixia could not be rejected for this species.

By combining the data from this study with those obtained for *A. anguilla*, we assessed the genetic differences between the two North Atlantic species using F_{ST} (Weir & Cockerham 1984), and, as expected, found the two species to be clearly distinct (overall $F_{ST} = 0.0176$; $p < 0.001$), and all interspecific pairwise comparisons were significant (table 1). A phenogram constructed from the D_{CE} pairwise distance matrix using a neighbour-joining algorithm (Saitou & Nei 1987) illustrated the distinction between the two species, and also revealed a tree topology for the American eel that reflects an absence of geographical structure, in contrast to the European eel (figure 2).

(c) *Population decline and climatic changes*

Major decisions concerning the management of both European and American eels require population parameters such as effective population size and temporal demographic changes that remain largely unknown. New tools based on Bayesian statistics and coalescence theory are now available (Beaumont 1999; Pertoldi *et al.* 2001; Storz & Beaumont 2002) to determine these from genetic data. Here, we used the procedure of Beaumont (1999) to detect population declines and expansions. Based on our previous study (Wirth & Bernatchez 2001), European eels were treated as three independent genetic units

Table 2. Pairwise sample differentiation estimates based on allelic variance at seven microsatellite loci in 21 North Atlantic eel samples.
(The first 13 samples belong to *Anguilla anguilla*, whereas the eight remaining samples belong to *A. rostrata*. Bold indicates significant θ estimates following Bonferroni corrections ($k = 210$, $\alpha = 0.05/210 = 0.000\,24$).)

samples	Minho	Couesnon	Tiber	Grand-Lieu	Elbe	Severn	Adour	Ölfus	Salses	Arresø	Motala	Imsa	St Johns	Wye	Medomak	Boston	South Edisto	Prince Edwards Island	Hudson	Trinité
Moulony	0.00242	−0.0009	0.0006	0.0007	0.0017	−0.0009	0.0017	0.0011	−0.0001	0.0027	**0.0076**	−0.0008	**0.0195**	**0.0183**	**0.0176**	**0.0190**	**0.0244**	**0.0199**	**0.0124**	**0.0298**
Minho		−0.0016	−0.0020	0.0005	0.0016	−0.0010	0.0008	−0.0008	0.0007	−0.0002	0.0039	0.0029	**0.0218**	**0.0203**	**0.0169**	**0.0219**	**0.0276**	**0.0206**	**0.0124**	**0.0307**
Couesnon			0.0001	0.0005	0.0022	−0.0008	0.0006	−0.0011	−0.0005	0.0020	**0.0080**	0.0032	**0.0186**	**0.0145**	**0.0140**	**0.0184**	**0.0244**	**0.0163**	**0.0125**	**0.0263**
Tiber				−0.0001	0.0046	−0.0002	0.0038	0.0014	0.0031	0.0021	**0.0110**	0.0030	**0.0174**	**0.0159**	**0.0159**	**0.0183**	**0.0234**	**0.0181**	**0.0113**	**0.0252**
Grand-Lieu					0.0003	−0.0016	0.0002	−0.0009	0.0016	0.0011	**0.0078**	0.0035	**0.0156**	**0.0118**	**0.0127**	**0.0158**	**0.0217**	**0.0145**	**0.0080**	**0.0231**
Elbe						−0.0002	0.0018	0.0016	0.0044	0.0003	**0.0044**	0.0044	**0.0196**	**0.0163**	**0.0175**	**0.0189**	**0.0254**	**0.0206**	**0.0161**	**0.0267**
Severn							0.0045	0.0005	0.0011	0.0037	**0.0094**	0.0037	**0.0189**	**0.0196**	**0.0171**	**0.0199**	**0.0262**	**0.0215**	**0.0133**	**0.0290**
Adour								0.0010	0.0026	−0.0013	0.0053	0.0022	**0.0216**	**0.0170**	**0.0148**	**0.0213**	**0.0271**	**0.0168**	**0.0148**	**0.0253**
Ölfus									0.0010	0.0035	0.0063	0.0036	**0.0140**	**0.0116**	**0.0096**	**0.0132**	**0.0179**	**0.0134**	**0.0070**	**0.0212**
Salses-Leucate										0.0036	0.0059	**0.0063**	**0.0217**	**0.0175**	**0.0177**	**0.0200**	**0.0295**	**0.0219**	**0.0153**	**0.0293**
Arresø											0.0004	0.0030	**0.0216**	**0.0151**	**0.0179**	**0.0199**	**0.0257**	**0.0204**	**0.0153**	**0.0272**
Motala												0.0078	**0.0360**	**0.0267**	**0.0297**	**0.0308**	**0.0397**	**0.0323**	**0.0215**	**0.0359**
Imsa													**0.0180**	**0.0153**	**0.0143**	**0.0163**	**0.0186**	**0.0170**	**0.0086**	**0.0211**
St Johns														0.0037	0.0005	−0.0016	0.0016	−0.0003	0.0020	0.0032
Wye															0.0034	−0.0008	**0.0073**	0.0022	0.0026	0.0026
Medomak																−0.0005	0.0033	−0.0002	0.0015	0.0011
Boston																	0.0018	0.0022	0.0010	0.0016
South Edisto																		**0.0070**	0.0002	0.0041
Prince Edwards Island																			0.0034	0.0031
Hudson																				**0.0052**

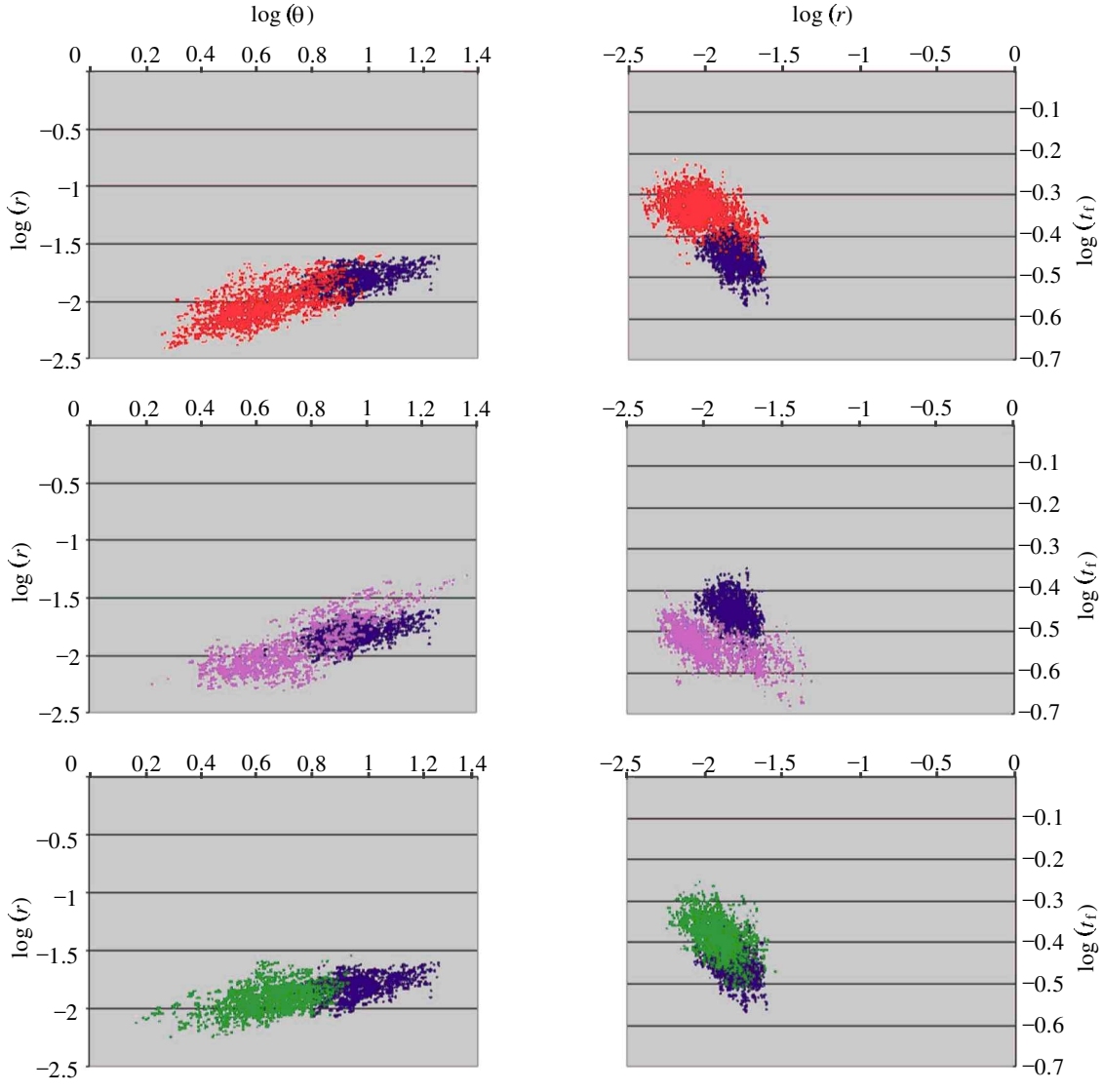

Figure 3. Plots of the marginal posterior distribution of log (r), log (θ) and log (t_f) for North Atlantic eels (18 000 updates). Blue dots correspond to *A. rostrata* samples, whereas the remaining colours correspond to *A. anguilla* samples (red, Atlantic samples; pink, Mediterranean samples; and green, North Sea plus Baltic Sea samples). Gene frequencies and simulations were based on a sample size of 100.

(Atlantic Basin, North/Baltic Sea and Mediterranean Sea) in order to reduce biased results caused by population mixing. All results clearly indicate a significant, two orders of magnitude, decrease in effective population size in recent historical times (table 2; figure 3). Based on a sexual recruitment age of 10–15 years (Tesch 1977), the onset of demographic decline between 766 and 5132 generations ago corresponds roughly to 8000–11 000 to 50 000–75 000 years. Moreover, the results clearly indicate differential dynamics between *A. rostrata* and *A. anguilla* populations. The decline has led to a more reduced contemporary effective population size within each of the *A. anguilla* subgroups than in *A. rostrata*, although the sum of the European eel stocks exceeds that of the American eel. Our results also indicate that the decline began earlier in North America than in Europe and that the rates of decline have been more pronounced in all three European stocks than in *A. rostrata*. Thus, the highest mean value of $r = 0.015$ (log $r = -1.818$) was observed for the American species, as was the highest effective population size (mean $N_0 = 9236$). This value is highly congruent with the previous estimate of female effective population size in *A. rostrata* of *ca.* 5500, which was derived from mitochondrial DNA data (Avise *et al.* 1988). These results were based on the exponential model of demographic change; however, a drastic decline was also detected with a linear demographic model, with the exception of an inflation of t_a.

Such dramatic declines could have been induced by large-scale events such as oceanic climate changes. The mean values for t_a are all close to 2000 generations, although slightly higher for *A. rostrata*. Assuming a mean generation time of 10 years, the onset of the observed decline corresponds to the last glacial maximum of the Wisconsinan glaciation. This glaciation had a direct impact on general ocean circulation in two major ways: by reducing the speed of the Gulf Stream (Duplessy 1999; Lynch-Stieglitz *et al.* 1999) and by moving the gyre boundary and associated currents further to the south (Keffer *et al.* 1988). Clearly, such changes would definitively affect the reproductive success of these species because the Gulf Stream is critical to transatlantic leptocephali migration. Alternatively, more recent climatic

changes such as the Younger Dryas (Lehman & Keigwin 1992; Keigwin & Jones 1994) cold event (11 000 years ago) could also have potentially initiated the demographic decline in both species as their confidence intervals on t_a overlap the timing of this cooling phase. However, our results suggest that the demography of the European eel was more severely affected, which could be a consequence of its longer pelagic phase and therefore greater dependence on Gulf Stream transport. Contemporary low effective population size estimates (5×10^3 to 10^4) show that *A. anguilla* and *A. rostrata* did not significantly recover from historical climatic changes, and European eel recruitment estimates of about 200 million eels annually must be downplayed as mortality of glass eels is close to 100% in some areas (Dekker 2000).

4. CONCLUSION

The future of both American and European eels remains unclear and the effects of global warming are still a matter of debate (Rahmstorf 1997), such that the impact of short-term changes in eel stocks remains difficult to estimate (Castonguay *et al.* 1994*b*). However, lessons learned from the past suggest that climatic changes that affect the Gulf Stream have an intricate effect on catadromous fishes. These observations therefore raise the possibility that climate-induced changes in the Gulf Stream circulation could result in another major man-induced environmental stress on eel demography, to add to the effects of the spread of *Anguillicola crassus*, an exotic nematode (Kennedy & Fitch 1990; Marcogliese & Cone 1993; Ashworth & Blanc 1997; Moser *et al.* 2001), surging glass eel prices and overfishing (Haro *et al.* 2000; Feunteun 2002).

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