

Recruitment Collapse and Population Structure of the European Eel Shaped by Local Ocean Current Dynamics

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Summary

Worldwide, exploited marine fish stocks are under threat of collapse [1]. Although the drivers behind such collapses are diverse, it is becoming evident that failure to consider evolutionary processes in fisheries management can have drastic consequences on a species' long-term viability [2]. The European eel (*Anguilla anguilla*; Linnaeus, 1758) is no exception: not only does the steep decline in recruitment observed in the 1980s [3, 4] remain largely unexplained, the punctual detection of genetic structure also raises questions regarding the existence of a single panmictic population [5–7]. With its extended Transatlantic dispersal, pinpointing the role of ocean dynamics is crucial to understand both the population structure and the widespread decline of this species. Hence, we combined dispersal simulations using a half century of high-resolution ocean model data with population genetics tools. We show that regional atmospherically driven ocean current variations in the Sargasso Sea were the major driver of the onset of the sharp decline in eel recruitment in the beginning of the 1980s. The simulations combined with genotyping of natural coastal eel populations furthermore suggest that unexpected evidence of coastal genetic differentiation is consistent with cryptic female philopatric behavior within the Sargasso Sea. Such results demonstrate the key constraint of the variable oceanic environment on the European eel population.

Results and Discussion

Oceanographic Modeling

We studied the effect of mesoscale currents and their variation on the European eel (*Anguilla anguilla*) over more than half a century using a novel high-resolution ocean model [8, 9], atmospherically driven with improved reanalysis products [10]. In silico, we released 8×10^6 virtual eels (v-eels) in an

area, depth, and time range reflecting the putative spawning area of the species [11, 12], allowing them to disperse [13] following realistic ocean conditions. This experiment was repeated annually for the period between 1960 and 2005. We subsequently defined v-eels as “successful” if they reached the continental shelf (25°W meridian) within a 2-year period within the simulation [14]. With this approach, we confirmed the existence of an ocean bifurcation pathway [15] that emerges only at sufficient spatial model resolution [16] and also a strong year-to-year variability in numbers at the European coastlines [17] (Figure 1). The north branch of the ocean bifurcation reflects the presence of European eel at high latitudes; the southern branch suggests the presence of eel larvae around the Canary Islands and Madeira, a prediction supported by field data [18]. The confirmation of such results provides an important demonstration of the resolution power of our novel model.

Owing to the extended period over which our model iterated variation in oceanic conditions, we were able to investigate the relative role of interannual to decadal oceanic variability on the eel recruitment: particularly, when comparing recruitment prediction from v-eels with actual observed recruitment available in International Council for the Exploration of the Seas (ICES) reports, the ocean model was strong in predicting both annual fluctuations and the collapse of observed recruitment ($F_{VR \times \text{time}} = 35.08$; $p < 0.001$; Figure 2). Interestingly, the significant interaction in our statistical linear model between v-eels and the period (before/after) of the major recruitment collapse shows that the correlation between oceanic fluctuations and eel recruitment was lost. Such significant interaction suggests that the lack of recovery in the European eel recruitment after the notorious decline was associated with other exogenous pressures such as parasites, pollutants, and/or lack of spawners [19–22]. Nonetheless, our study gives conclusive evidence for an oceanographic onset of the recruitment decline of the European eels.

Our analyses also revealed that years showing high dispersal rates were characterized by predominantly westward currents in the variable flow regime east of the Bahamas [23], providing a “shortcut” of the much longer route to the Gulf Stream through the Caribbean Sea. In those years, a large fraction of the v-eels can reach the Gulf Stream in a matter of weeks (Figure 1). In years with lower dispersal rates, the shortcut was absent, so that v-eels could only follow the extended migration route through the Caribbean Sea. We identified that the existence of the shortcut is dependent on the regional wind characteristics shaping the details of the western part of the subtropical gyre (see Figure S1 available online). Note that the general spreading pattern is not significantly affected by depth of v-eel release (e.g., 300 m) or longer dispersal periods (e.g., 3 years) (data not shown).

The spatial and temporal variability of the currents observed in the Sargasso Sea revealed that the spawning ground of the European eel was highly dynamic and that such variation strongly affected eel recruitment (Figure S1). What, then, are the consequences of such heterogeneous environments on genetic structure in coastal Western European eel populations? This question is important because conflicting reports

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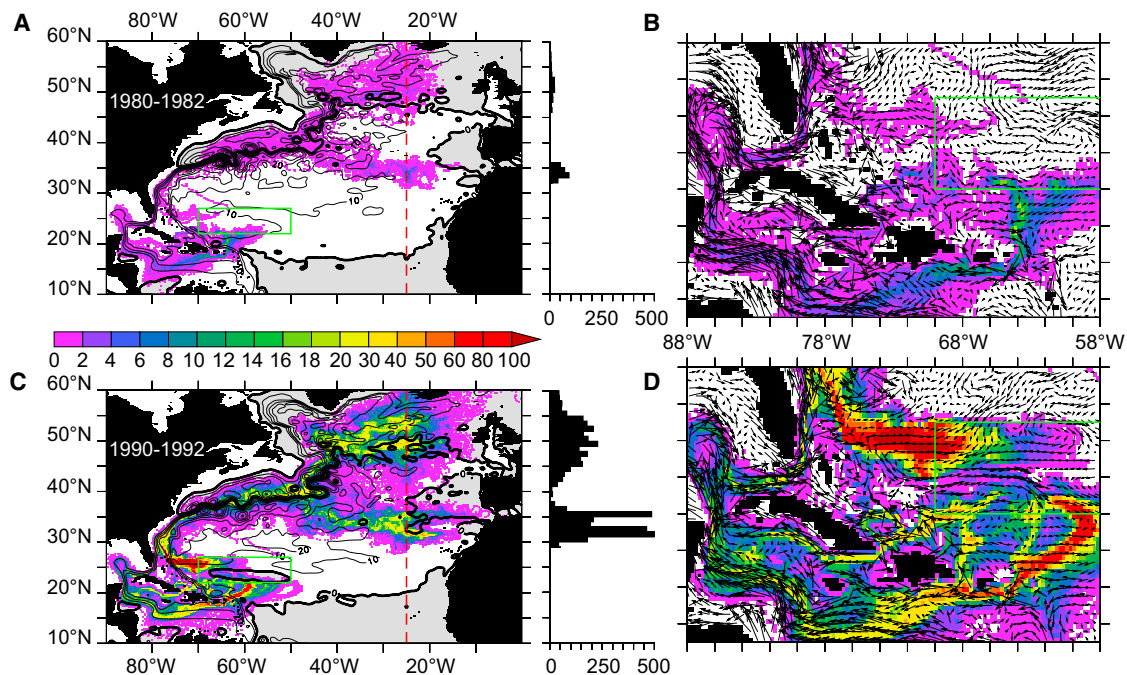


Figure 1. Simulated v-Eel Dispersal Rates

(A and C) Examples of low (A; 1980–1982) and high (C; 1990–1992) dispersal rates (in 10^{-2} eels/m²) from the released area (50°W–70°W; 22°N–27°N) in the Sargasso Sea (green box) toward 25°W within 2 years. Oceanic circulation is contoured by the horizontal stream function (1-year average). Histograms show the number of v-eels arriving at 25°W, binned at 1° resolution and summed over the first 100 m of the water column.

(B and D) Close-up of dispersal rates and ocean currents, averaged over the first 3 months after release for low and high years.

regarding the existence of a panmictic breeding system in eels have raised questions regarding the existence of a single, randomly mating population. Such conclusions have also important implications for conservation and fisheries management, as numerous early-life-stage eels are translocated among watersheds in order to support fisheries, possibly affecting sensory cues required to return to the Sargasso Sea [18, 24].

In Silico Population Genetics

We first examined this question in silico by (1) generating two genetically distinct spawning scenarios—panmixia versus female philopatry (Figure S2)—within the high-resolution ocean circulation models and (2) comparing genetic signatures of artificially created populations at the 25°W meridian. Overall analysis showed that under the scenario of panmixia, no spatial or temporal genetic structure was detectable on European coasts (analysis of molecular variance [AMOVA]; 99% of overall variation within all populations; $p < 0.001$). Conversely, the scenario of female philopatry constrained the distribution of both spatial (among sites within years = 1.2% of overall variability, $p < 0.01$) and temporal (among release events = 8.6% of overall variation, $p < 0.001$; within continental sites, among release events = 9.8% of overall variation, $p < 0.001$) genetic variability in European populations (Tables S1A and S1B).

In spite of a homogenizing effect of the ocean, the overall degree of in silico estimated F_{ST} differentiation was higher under the female philopatry scenario than under panmixia (panmixia $F_{ST} = 0.01 \pm 0.006$ [SEM]; female philopatry $F_{ST} = 0.03 \pm 0.01$; $t = 2.14$, $df = 12.65$, $p = 0.05$). Interestingly, spatial pairwise comparisons among continental v-eel populations (Table S2) revealed that observable genetic structure can result from both the panmixia and female philopatry scenarios, especially

in years of low recruitment. Those structures were not linked to any obvious form of isolation by distance (all Mantel tests $p > 0.001$; Table S3). Pairwise comparisons (Table S2) of modeled genetic structure across different temporal periods also revealed significantly higher genetic differentiation under female philopatry than under panmixia (Student's test; $t = 5.49$, $df = 7.26$, $p < 0.0001$), suggesting that a nonpanmictic mode of evolution may result in an isolation by time [6]. Considered together, our results unify previous conflicting reports regarding the evidence for a panmictic mode of reproduction in European eels, as even under this mode of evolution, under low recruitment conditions, departure from signature of random mating can exist on European coasts [6, 7, 25]. Our model outputs provided support for the hypothesis that the genetic signature of spatially structured (or even panmictic) distribution within the Sargasso Sea should be reflected as observable genetic structure in eels recruiting to European coastal populations.

Because the relative number of successfully arriving v-eels produced by each event was negatively correlated with the mean F_{ST} values associated with the female philopatry scenario (Spearman rank correlation: $\rho = -0.69$, $p = 0.04$), we predict that any observed genetic structure will be stronger under conditions of low recruitment. No such relationship was observed under the scenario of panmixia (Figure S2).

Molecular Analyses of Natural Populations

After our in silico examination of the role of different modes of reproduction in v-eel populations, we tested for signatures of genetic structure in natura based on the hypotheses emitted from the ocean current models. Hence, we sampled yellow-phase eels from contemporary populations from 13 different

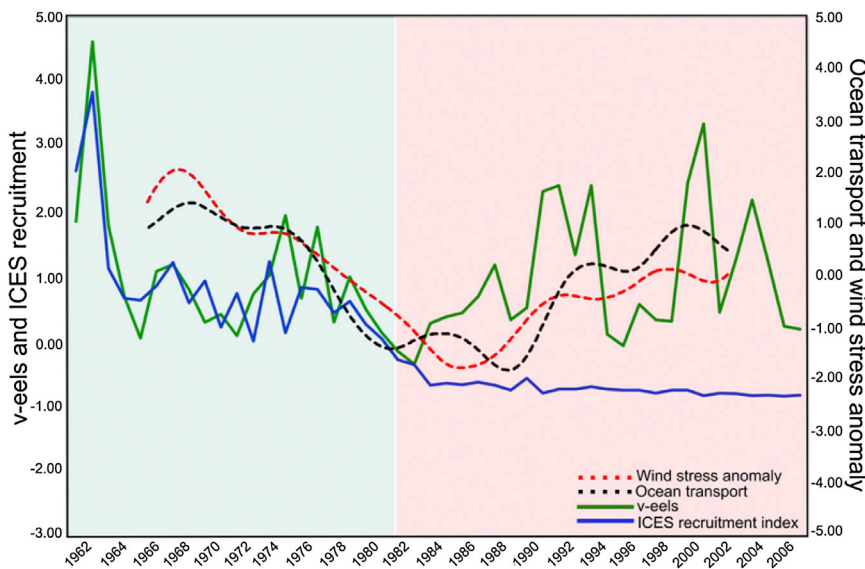


Figure 2. Natural Recruitment, Simulated Virtual Recruitment, and Wind Forcing between 1962 and 2007

Left y axis: ICES-NS natural recruitment index (blue curve) and virtual recruitment (v-eels, green curve). Right y axis: ocean transport (dashed black line) at 70°W, integrated between 24°N and 27°N. The wind stress anomaly (dashed red line) was integrated between 24°N and 28°N and between 60°W and 50°W (values were multiplied by -1 for representation purposes). For transport and wind stress, a 121-month Hanning filter was applied to focus on decadal timescales.

sites located along the natural marine-freshwater salinity gradient inhabited by this species [26]. This strategy was devised to screen variation across both large and small geographic scales. We assessed polymorphism of the *ND5* region of the mitochondrial genome (which should best reflect female-mediated structure such as philopatry) as well as 17 nuclear loci (which should provide a more contemporary picture of mating systems). Information on natural populations can be found in Table S5. Consistent with some of the previous findings using nuclear markers [5, 6], we found weak but significant genetic structure among some sampling locations (Table S6). More striking however, was the strong and significant genetic structure detected using the maternally inherited mtDNA (Figure 3A; Table S6), which was significantly higher than that shown using nuclear markers (mtDNA $F_{ST} = 0.11 \pm 0.002$ [SEM]; microsatellites $F_{ST} = 0.02 \pm 0.0001$; $t = 7.96$, $df = 9$, $p < 0.001$). Although this pattern may arise from slower allelic fixation of microsatellites and a 4-fold higher effective population size of nuclear DNA (nDNA) compared to mtDNA [27], lower levels of nuclear differentiation are generally thought to arise from female structured populations and male-mediated gene flow through opportunistic mating [28]. Deeper investigations on mtDNA gene phylogeny showed multiple lines of evidence supporting the existence of subpopulations at the source location (Figures 3B and S3; Tables S5, S6, and S7).

Importantly, the overall order of magnitude of F_{ST} detected via mtDNA sequencing reflected the higher F_{ST} levels predicted from our in silico scenario simulating female philopatry. This correlation and the maternal inheritance of mtDNA [29] suggest the discovery of a previously unreported mode of reproductive behavior in the European eel, where females are philopatric to and within locations in the Sargasso Sea, whereas males maintain gene flow by returning earlier than females to the spawning ground where they may mate opportunistically [18, 30]. Although the mechanisms underlying the homing behavior in this species are not well understood [31] and may be linked to the Earth's magnetic field [24], life history strategies of this kind are common both in aquatic and terrestrial organisms [28, 32].

In summary, a process of atmospherically driven dispersal by ocean currents connects the putative spawning grounds of the European eel and the Gulf Stream, greatly enhancing

the arrival of juveniles at the European coast. When atmospheric-oceanographic conditions shift and this mechanism is absent, eel recruitment is low, explaining the onset of the large-scale collapse in recruitment that occurred during the 1980s. Following the crash, the capacity of the eel population to recover not only was limited by a reduced supply of potential recruits but was further diminished by the effects of a multitude of anthropogenic impacts, combining to limit the probability of recovery of this ecologically and economically important species. To compensate for the shortage of eels in European freshwater systems, management measures such as stocking of eels across large geographical scales have been put in place. The assumption of a panmictic breeding system was thought to limit any consequences of such movement of individuals, but our work suggests that this may have unexpected impacts and furthermore may affect the recovery of this species. Finally, our work highlights the potential power of combining oceanographic modeling with modern population genetics, and the fusion of the two approaches will likely represent a valuable tool to understand the fundamental basis of species' evolutionary biology and ultimately optimize conservation programs.

Experimental Procedures

Oceanographic Modeling

We investigated the effects of oceanographic variability along the known dispersal pathway connecting the European eel's spawning grounds (Sargasso Sea) and the European coast by utilizing a global ocean circulation model with a very high resolution ($1/20^\circ$, ~ 4 to 5 km grid size) in the North Atlantic between 32°N and 85°N (VIKING20), accomplished by a two-way nesting approach [8] into the ORCA025 model [33] based on the NEMO code [9]. Owing to its very high resolution, which was identified as an important prerequisite for a realistic simulation of eel dispersal [16], advanced numerics [34], and a synoptic atmospheric forcing of the period 1948–2007 [10], our model allows the investigation of spatiotemporal variability of oceanic circulation influences with much improved verisimilitude. A detailed description of the VIKING20 ocean model is provided in the Supplemental Experimental Procedures and Figure S4. In short, using a Lagrangian tracking technique [13], we released 8×10^6 virtual eels (v-eels) in an area and depth range reflecting the putative spawning area of the European eel [11, 12], following results and discussion for vertical distribution in [14]. Release was performed during the month of May (from the 1st until the 31st) [35]. We then calculated the dispersion of the v-eels with the transient three-dimensional flow field of the base model. The procedure was repeated for every year during the 1960–2005 period. Particles reaching the eastern North Atlantic (25°W) within 2 years of advection were defined as successful migrants [14] and entered subsequent recruitment and genetic analyses.

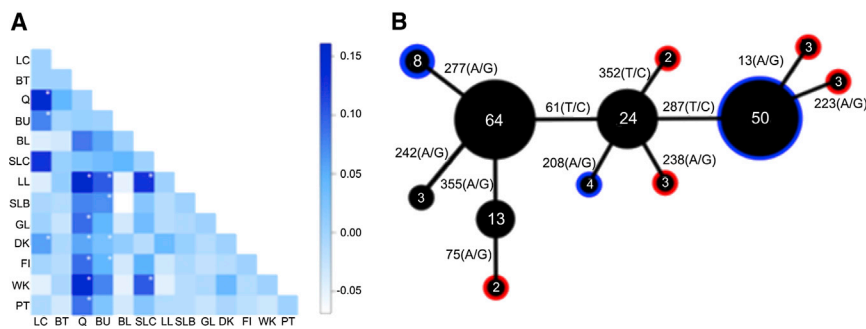


Figure 3. Observed Genetic Differentiation and Phylogeny in the mtDNA Gene

(A) mtDNA pairwise comparison matrix among 13 eel populations here represented as a heatmap (Arlequin v3.5 R graphical interface). White asterisks identify pairwise locations shown to differ significantly in haplotype composition. Significant F_{ST} values ranged between 0.058 (Q/DK) and 0.16 (Q/LL).

(B) Phylogeny and haplotype relationships are shown here in the format of a simplified haplotype network (no unique haplotypes). Numbers inside each haplotype represent that haplotype's frequency; branching numbers represent polymorphism defining the haplotypes. Red and blue markers reflect the neighbor-joining tree; blue = 50 < bootstrap < 60; red = 60 < bootstrap.

Virtual and Natural Recruitment

The hypothesis that ocean currents drive European eel recruitment and decline was tested by the statistical comparison of natural [36] and virtual recruitment. The recruitment data set used in this study corresponded to generalized linear model of recruitment for the North Sea, hereafter referred as "ICES," as it incorporates the longest recruitment index for the European eel, Den Oever [36]. Both types of recruitment were standardized to their z scores for direct comparisons. For statistical purposes, we defined "decline" as the time point where natural recruitment z scores became consistently negative; the factor "time" was introduced to delimit the periods "before" and "after" the population collapse. The relationship between natural and virtual recruitment before and after the decline was inferred by linear models run in R [37]. Ocean transport and wind forcing were also standardized to their z scores.

In Silico Population Genetics

We integrated the eel genetic component to the oceanic model by splitting the released particles into ten different mtDNA haplotypes. These haplotypes were distributed either randomly or along ten subareas within the Sargasso Sea. Here, we aimed to simulate the consequences on eel distribution at continental sites of a panmictic spawning ground versus a contrasting scenario of complete genetic structure which would correspond to the population signature of female philopatry within the spawning ground. Subsequently, successfully arriving (i.e., within the 2-year period) v-eels were split, on the European coast, into an equal amount of ten populations—each population spanning 4° latitude (Figure S2). To discriminate any effects of temporally and spatially isolated samplings on genetic structure under both spawning scenarios, we performed two AMOVAs: (1) among release events and (2) among artificial populations at continental sites. The capacity of the release events to generate genetic structure at the coast was also examined by calculating Wright's index (F_{ST}) pairwise comparisons among artificial populations. Isolation by distance was calculated among artificial populations. To this end, geographical distances were converted according to the relation 1° latitude = 110 km. Finally, to investigate the possible link between recruitment and population structure at continental sites under the proposed spawning scenarios, we correlated each release event's averaged F_{ST} with the proportion (Table S1) of successfully arriving particles.

Molecular Analyses and Populations Genetics

The presence of genetic structure among European eel coastal locations was evaluated by sampling yellow eels spanning 13 locations (Table S2A) across both small (within Ireland) and large (additional four continental sites) geographical scales. A total of 240 individuals were examined for a section of the ND5 (355 bp) mitochondrial gene as well as 17 nuclear loci. Population structure was assessed through calculation of F_{ST} values between populations. We also added eight American eel (*A. rostrata*) sequences to test for neutral evolution of the mitochondrial marker. Detailed descriptions of molecular protocols, analyses, and software used are given in the Supplemental Experimental Procedures.

Supplemental Information

Supplemental Information includes four figures, seven tables, and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2013.11.031>.

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