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Running head: Eels stocking experiment and demography

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Abstract

1. Since the 1980’s, the European eels stocks have dramatically decreased with no sign of recovery resulting in their classification as Critically endangered on the IUCN red list of threatened species.
2. The European Council Regulation 1100/2007 requires that 35% of glass eels caught annually by fishing be released in European waters for restocking. However, the efficiency of this measure on population viability has never been evaluated.
3. Here, we estimated demographic parameters of a stocked population of French eels using a multistate capture-recapture model. Using these estimates, we then estimated population size and predicted the number of future genitors obtained by stocking.
4. We found that the stage in which eels were stocked did not influence their future survival and that the maximal number of silver eels was quickly reached, after 3 years following stocking.
5. We concluded that stocking experiments in the Mediterranean region are efficient for fast production of genitors. We suggest that further studies should assess the quality of these genitors.

Introduction

The European eel (*Anguilla anguilla*) is one of the scarce freshwater species widely fished by professional fishermen. Its fishing represents crucial economic incomes for European fishermen that make the future survival of the species a major concern. However, since the 1980's, a 50% decline in European eels stocks and an up to 99% decrease in glass eel (life stage attained when larvae reach the European coasts) recruitment have been observed on the whole distribution area (Feunteun, 2002; ICES, 2010) with no sign of recovery. Several causes for this decline have been proposed such as climatic variation, habitat loss (Kettle *et al.*, 2011) and degradation (by the placement of barriers in the migration routes such as dams, sluices, and gauging structures), pollution with PCB's, infections with the swimbladder parasite and overfishing (Pujolar *et al.*, 2011). As a result, the European eel has been classified as critically endangered in the IUCN Red List of Threatened Species.

To encourage the recovery of the European eel stocks, the European Council Regulation (No 1100/2007 published in September 2007) required all member states that contain natural habitats of the European eel to establish eel management plans. The objective was to enable the escapement to the sea of at least 35% of the silver eel biomass, relative to the pristine estimated stock levels (i.e. pristine recruitment levels) and in the absence of human influences. To do so, several measures have been proposed including, among others, restocking. The aim of restocking is to supplement the existing population by producing more silver eels (also referred to as genitors) from the addition of young eels to a water body from another source. Mediterranean wetlands are good candidates for such experiments because eels growth is faster than in central and northern Europe (Acou *et al.*, 2003; Svedäng *et al.*, 1996) and the distance to the Sargasso Sea (the reproduction area) is much smaller than from northern Europe.

However, very few studies have been conducted to demonstrate the effectiveness and suitability of such measure. In particular, there is a lack of quantitative studies that would help in formulating advice on if, when, where and how much to stock (WGEEL2009, 2010). In this context, the use of population dynamics tools for estimating demographic parameters is crucial in population management. It allows the assessment of the population variation over time, as well as the evaluation of the impacts of management practices and the effectiveness of conservation strategies, which is especially important in the case of a critically endangered species.

In 2007, a conservation stocking experiment was launched in the marsh Vigueirat in south-east of Arles (France) to assess the long-term restocking efficiency in producing silver eels of good quality (with none or low prevalence of the parasite *Anguillicoloides crassus* (Palstra *et al.,* 2007), low pollutant's load, especially PCBs and cadmium (Pierron *et al.*, 2008; Palstra *et al.,* 2006), and high lipid content (> 20%, Belpaire *et al.,* 2009)). Glass eels and individually marked elvers and yellow eels from different origins were stocked to evaluate the potential number of future genitors (silver eels) and their biological quality. The first step in doing so was to quantify survival and transition between stages in this population. However, estimating survival and life stage transitions is difficult because not all individuals can be captured (Gimenez *et al.,* 2008). Besides, stage-related individual heterogeneity in the detection process can lead, if ignored, to inaccurate estimates. In this study, we used a multistate capture-recapture model (Lebreton *et al.*, 2009) to estimate stage-specific survival and transition rates between stages and identified factors affecting these parameters while accounting for detection less than one. These results were then used to assess the eel stocking experiment efficiency by a) estimating population size and b) predicting the number of silver eels obtained by stocking.

Material and methods

Study species

The European eel (*Anguilla anguilla*) is a catadromous and semelparous fish. Born in the Sargasso Sea, the larval-stage eel drift across the Atlantic Ocean towards the Mediterranean Sea on the current of the Gulf Stream and North Atlantic Drift. Whenever approaching the Mediterranean shores, they go through metamorphosis into glass eels (between January and April, Lefebvre *et al.*, 2003) at 350 days to 2 years of age on average (Kettle & Haines, 2006; Wang & Tzeng, 2000). As glass eels migrate upstream, they progressively become more pigmented, or ‘elvers’, and after a few months, develop into ‘yellow eels’. This stage is characterized by a growth stage during which eels become relatively sedentary. Yellow eels spend the next years (3 to 8 years for males and 5 to 12 years for females) feeding and growing. Whenever mature, they start their downstream migration to the ocean for spawning (Tesch, 2003) as ‘silver eels’.

Study area

The ‘Pisci-Sud’ freshwater pond (salinity = 0 g/L) is located in the Vigueirat marsh in south-east of Arles, River Rhône Delta (France). It is a 32 ha basin which is totally closed preventing eels stocked from escaping. The basin is divided into a dense reedbed of 20.5 ha and two closed interconnected ponds of 6 ha and 50 cm deep and 5.5 ha and 25 cm deep. According to previous isotopic studies, eels main preys in Piscisud were chironomids, the fish Pseudorasbora parva and the Louisiana crayfish Procambarus clarkii (unpublished data). The period during when eels were active in the basin (temperature above 8°C) varied between 177 and 249 days a year with a mean temperature between 19,05 and 19,63°C.

Data collection

In October 2007, three groups were stocked (Table 1). Groups Vacc1 and Vacc2 were collected from the brackish Vaccarès lagoon (salinity = 22.0 ± 2.9 g/L) whereas group Grau1 was collected from a freshwater canal (salinity = 1.8 ± 0.09 g/L) near Grau de la Fourcade fish-pass (Crivelli *et al.*, 2008). Eels belonging to groups Vacc1 and Grau 1 were < 300 mm long whereas eels from the group Vacc2 were > 300 mm long. Silvering stages of stocked eels were assigned according to the EELREP index (Table 2) based on length, weight, eye diameter and pectoral fin length. All individuals from groups Vacc1 and Grau1 were classified as sexually undifferentiated eels while individuals from group Vacc2 were classified as yellow eels (most) and sexually undifferentiated eels. Prior stocking, eels were individually marked with transponders (PIT tags). Beginning in January 2008, 2.5 kg of glass eels captured from the Grau de la Fourcade fish-pass were stocked each year (Table 1) and batch marked with tetracycline.

Two samplings consisting of nine consecutive days, in April-May and October, were conducted each year from 2008 until May 2011. Eels were captured by passive trapping using different nets: six "capetchades" nets (which consist of a barrier leading into an enclosure surrounded by 3 trap nets and which keep alive the fish and shell-fish which get into them) with a 6 mm mesh size in the funnel and a leading net of 40 m, 13 fyke nets with a 6 mm mesh size, and 5 capetchade nets with a 0.5 mm mesh size in the funnel and a leading net of 20 m. The use of different mesh sizes allowed the capture of all eels regardless their sizes (Bevacqua et al., 2007; 2009). The nets were arranged at the same location for each sampling and were visited every morning. The fishing effort for one sampling period was equal throughout the years. All captured eels were anesthetized with phenoxyethanol, measured, weighed and their EELREP stage determined. To check whether the individual was already marked, we used a handheld reader which reads radio frequency identification tags. If unequipped and <160 mm length, eel was marked by caudal fin removal or, if >160 mm, with PIT tag. Migrant eels (Table 2) were sacrificed for analyses to determine the future genitor quality (parasite *Anguillicoloides crassus* presence, pollutants and lipid content). Captured eels were placed in a net until the end of the sampling period and were released in Pisci-Sud the last day of the sampling period.

Data analysis

Data were analyzed using multistate capture-recapture models (Lebreton *et al.*, 2009) considering four different stages: sexually undifferentiated eels (E), yellow eel (Y), silver eel (S) and dead eel (D). The temporal dynamics of stages was governed by transition probabilities (ψ). For females, we considered transitions from sexually undifferentiated eels to yellow eel and from yellow to silver eel. For males, as transitions from sexually undifferentiated eels to yellow eel and then from yellow eel to silver eel occur too quickly for being seen in the field, we only considered a direct transition from sexually undifferentiated eels to silver eels. A yellow eel could not return to the sexually undifferentiated eels stage: transition probability from stages Y to E was fixed to 0. Similarly, a silver eel could not return to sexually undifferentiated eels or yellow eel stage but remained silver eel. Transition probabilities from S to E and Y were fixed to 0 while the one from S to S was fixed to 1. These transitions were conditional on survival probability (Φ) and stages were related to observations through detection probabilities (p).

We defined a set of candidate models incorporating biologically relevant combinations of time (representing temporal variation between sampling periods, i.e. 6 months), stages and group effects on survival, transition and detection probabilities. Regarding temporal effects on survival, we considered continuous and seasonal effects to test for the influence of weather. We incorporated a group effect to assess whether the stage in which eels were stocked influenced their survival. We examined the stage effect on survival as it was suspected to differ between sexually undifferentiated eels, yellow and silver eels. Regarding recapture probabilities, we considered temporal effect and because silver eels were supposed to be less sedentary than in other stages due to their need to migrate downstream to the sea, we tested for an influence of stage. We did not consider an effect of group on recapture probability because sampling effort did not vary (passive trapping).

We incorporated these effects on each parameter (p, Φ and ψ) sequentially while constraints on remaining parameters were held constant. Once the main effect was determined for a parameter, we added each of the remaining effects in an additive and interactive fashion to assess if one of these combinations was relevant and we repeated this until no better model was selected. We started by identifying the most appropriate structure for p, then for Φ using the previously selected structure for p and finally for ψ

using the structures for p and Φ selected in the previous steps. In total, we fitted 68 models (See Table S1 in Supporting Information) and selected the most parsimonious model using AIC (Burnham & Anderson, 2002).

These analyses were performed with program E-SURGE (Choquet *et al.*, 2009a). In addition, we assessed the quality of fit of multistate models (Pradel *et al.*, 2003) using program U-CARE (Choquet *et al.*, 2009b).

We estimated abundance N_i at sample occasion i, as $n_i / \hat{p}_i$, where n_i is the number of eels recaptured and $\hat{p}_i$ is the estimated detection at the occasion i. Approximate 95% confidence intervals were calculated as $\hat{N}_i \pm 2 \text{x} SE(\hat{N}_i)$, where $SE(\hat{N}_i) = n_i \, (SE(\hat{p}_i) / \hat{p}^2)$.

We predicted the number of silver eels obtained by stocking as follows. Eels become migrant silver eels between 2 and 12 years in the Mediterranean region. Hence, we focused on the number of silver eel obtained between 2 and 12 years after stocking starting with 100 sexually undifferentiated eels. The fate of individual was determined based on repeated Bernoulli trials for survival and multinomial trials for transition between states, using the stage-specific estimates obtained from the best model. Our best supported model including time effect on both survival and transition (see results), we used the mean survival and transition probabilities of each stage for the simulations. Demographic stochasticity was accounted for by repeating this process 1000 times. These analyses were performed in program R (R Development Core Team 2009).

Results

The goodness-of-fit test result stated that we could not reject the null hypothesis that the model fits the data adequately ($\chi^2 = 64.21$, df = 59, P = 0.30). Parameters were estimated on a 6 months interval (interval between two samplings period).

The best model according to AIC (See Table S1) suggested that recapture probabilities varied with stages and time. Silver eels had a higher recapture probability than other stages (Table 3) (except in October 2009 and 2010).

Survival probabilities did not depend on group but differed according to stages. Time also influenced survival probabilities (Fig.1). Indeed, survival of sexually undifferentiated eels and yellow eels was lower during the spring/summer (April to October) than in autumn/winter (from October to April). However, in October 2010, survival of both sexually undifferentiated eels and yellow eels was extremely low. Because three out of six probabilities were estimated to 1, the boundary of the domain of definition of a probability, it was difficult to determine a trend in the survival of silver eels. These estimates on the boundary can be explained by the fact that all silver eels survived over the time interval. As a consequence of no variation in the survival outcome, standard errors could not be estimated.

Transitions between stages were influenced by time, group and states (See Table S1 and Table S2 in Supporting information). Transition probabilities from sexually undifferentiated eels to yellow eels (females only) were higher than transition probabilities from sexually undifferentiated eels to silver eels (males only) whatever group and sampling period (Fig. 2). Transition probabilities of eels stocked as glass eel (groups Grau 08, Grau 09 and Grau 10), were null during the next few months after stocking (Fig.2) but then increased with time. For individuals stocked as sexually undifferentiated eels (groups Vacc1 and Grau1), transition probabilities increased first, then fluctuated between sampling periods. Indeed, transition probabilities were higher during spring/summer (from April to October) than during autumn/winter (from October to April). Finally, transition probabilities of bigger stocked individuals (>300 mm) (group Vacc2, mostly composed of yellow eels) showed oscillations between seasons.

Population size was estimated for each eel stage and for each sampling period from April 2008 to May 2011. The number of sexually undifferentiated eels was higher than the number of yellow eels which was higher than the number of silver eels (Table 4). The number of sexually undifferentiated eels oscillated with the season. Indeed, the number of individuals was higher in spring than in the following autumn. The number of yellow eels increased constantly with time. However, the number of silver eels decreased since October 2009.

Numbers of future genitors were predicted for groups Vacc1, Vacc2 and Grau1. These groups were chosen as representative because their individuals were old enough when they were stocked for their transition probabilities to have reached the oscillation regime. We assumed this regime to be representative of the trend in transition probabilities because it reflects behavioral changes between seasons (see discussion). Mean cumulative number of silver eels quickly reached a plateau starting between 3 and 5 years and after 12 years, between 10 and 14 silver eels were obtained (Fig. 3).

Discussion

The analysis of stages' dynamics provides a powerful tool for evaluating stocking experiments by determining the demographic parameters of the stocked population and predicting spawner production. We applied this approach to the European eels which has, to our knowledge, never been done before.

Recapture

Recapture probabilities were low and varied with stages and time. Our estimates showed that silver eels had, in general, a higher recapture probability than sexually undifferentiated eels and yellow eels. This might be explained by the fact that individuals were captured using passive nets. As a consequence, the more mobile an eel was, the more it was likely to be recaptured. Because silver eels were trying to migrate downstream to the ocean (Tesch, 2003), they were more prone to be recaptured in the fishing nets. The very low recapture probabilities of yellow eels were consistent with the fact that this stage is considered as the most sedentary and territorial stage within the whole eel lifecycle (Lafaille *et al.*, 2005). As yellow eels were stocked in October 2007, they could still look for a territory in April 2008 which might explain the higher recapture probability in this sampling period. Recapture probabilities also varied between sampling periods. Weather might be the main cause of these fluctuations, drop in water temperature reducing movements and therefore catches (Riley *et al.* 2011) and rain and wind having positive effect on recapture probabilities.

Survival

We did not detect any influence of group on survival probability. This provided evidence that stage in which eels were stocked did not influence their future survival.

Therefore, instead of only reserving glass eels for restocking, older eels (e.g. yellow eels) captured could also be restocked to produce genitors faster. Indeed, yellow eels become silver eels faster than glass eels that need more time to mature. However, we found evidence that survival probabilities were influenced by stages and time. Indeed, survival of sexually undifferentiated eels and yellow eels was lower during the spring/summer period (April to October) than in autumn/winter (from October to April). This is coherent with the fact that during the cold months of winter, eels were immobile and did not feed (Panfili *et al.*, 1994). This long fast might make the spring/summer period crucial for eels survival since individuals had to build up their fat stores again during this period.

In October 2010 both sexually undifferentiated eels and yellow eels survival were extremely low. This might be a consequence of a negative density-dependence effect due to the stocking of 2.5 kg of glass eels each year (Acou *et al.*, 2011; Lobón-Cerviá & Iglesias, 2008). To check this hypothesis, analyzes of the recapture data from the last sampling periods should be done.

We could not determine a trend in the survival of silver eels because of half probabilities estimated on the boundary.

Between-stage transitions

We first showed that probabilities of transition from sexually undifferentiated eels to yellow eels (females) were higher than probabilities of transition from sexually undifferentiated eels to silver eels (males). This indicated that most eels in Pisci-Sud were females. This was expected as sex is mainly determined by eel density, with low (resp. high) densities favoring females (resp. males) development (Melia *et al.* 2006; Tesch, 2003). High proportions of females are generally found in rivers where densities are low, whereas males tend to dominate estuaries and lagoons where densities are high (Tesch, 2003; Walsh *et al.*, 2004).

Different regimes of transition probabilities were observed. For eels stocked as glass eels or sexually undifferentiated eels (groups Grau08, Grau09, Grau10, Vacc1 and Grau1), the probabilities increased during the first years after stocking without being influencing by a season effect (Fig.2). Then, the probabilities fluctuated between sampling periods as the transition probabilities for eels from Vacc2. Indeed, transition probabilities were lower in autumn/winter than in spring/summer. During winter, eels were immobile and did not feed (Panfili *et al.*, 1994). Consequently, growth was slackened during these periods and transition probabilities between stages were lower or null (as the growth is directly linked with the stage assigned to an eel (Table 2)). Two hypotheses could explain the first increase of the probabilities. First, eels might be more active when they were young (whatever the stage they belong) and kept feeding during autumn/winter. Thus, they kept growing and their probabilities of transition increased with time. However, once they reached older ages, eels became more sedentary and were influenced by the season. As we did not know the age of eels, we could not confirm this hypothesis by testing for an age effect. The second hypothesis is that stocking could be a stress factor modifying the behavior of young eels (glass eels and sexually undifferentiated eels) during the first months after stocking.

Population size and predicted number of silver eels

Since the stocking experiment has started, the number of eels in old stages has remained lower than the number of eels in younger stages. Firstly, this can be explained by the fact that a lot of eels have not reached the older stages (yellow eels and silver eels) yet. Secondly, because of the lower survival probability of sexually undifferentiated eels and yellow eels during spring and summer, most eels will never reach the silver eel state. The number of sexually undifferentiated eels estimated in Pisci-Sud was higher in early spring than in the following autumn. This is consistent with the fact that the survival of sexually undifferentiated eels was lower during spring/summer than during winter. Unlike sexually undifferentiated eels, the number of yellow eels constantly increased with time. This might be explained by high transition probabilities from sexually undifferentiated eels to yellow eels (Fig. 2). However, the number of silver eels decreased since October 2009. This was due to the fact than most of the individuals from the first groups of eels stocked in Pisci-Sud (Vacc1, Vacc2 and Grau1) have already reached the silver eel stage whereas eels from more recent groups (Grau 08, Grau 09 and Grau 10) haven't yet.

Regarding predictions, from 100 sexually undifferentiated eels initially stocked, between 10 and 14 silvers eels were obtained between 3 and 5 years after stocking. This is consistent with a previous study (Acou *et al.*, 2003) that found that silver eels production in the Mediterranean region is fast (from 3 to 6 years) compared to the north European environment (Svedäng *et al.*, 1996). Further work is required to estimate the number of silver eels obtained from eels stocked as glass eels (groups Grau08, Grau09 and Grau10). We anticipate that stocking projects in the Southern Europe may be more effective in increasing the number of genitors.

In conclusion, we estimated demographic parameters of a stocked population of eels using multistate capture-recapture modeling. These estimates allowed predicting numbers of future genitors. We encourage further studies (determination of lipids and pollutants concentration and evaluation of the parasite load) to assess the quality of these genitors.

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Table 1: Information about the European eels stocking at Pisci-Sud.

Table 2: Protocol for determining stages according to EELREP (2005). The so-called silver index[*] allows determining the 'degree of silvering' of eels (*Anguilla anguilla*). There are five stages for females and two for males. An eel was considered as 'sexually undifferentiated eels' when its EELREP stage was missing (which occurred when an eel was too small for its EELREP stage to be determined) or I, 'yellow eel' when EELREP stage was FII or FIII and 'silver eel' for EELREP stages FIV, FV and MII.

Table 3: Recapture probabilities according to state and sampling occasion (with lower (CI-) and upper (CI+) limit of the 95% confidence interval and standard error (SE)).

Table 4: Eels population size estimates according to stage and sampling period with lower (CI-) and upper (CI+) limits of the 95% confidence interval and standard error (SE).

Figure legends

Fig. 1: Survival probabilities (with 95% confidence interval) according to stages and time. A "*" indicates estimates on the boundary.

Fig. 2: Transition probabilities (with 95% confidence interval) for eels from groups Grau08 representative of eels stocked as glass eel, Grau1 representative of individuals

stocked as sexually undifferentiated eels and Vacc2 representative of individuals stocked with length > 300 mm (mostly yellow eels).

Fig. 3: Prediction of mean number of silver eels obtained from 100 sexually undifferentiated eels according to time and group: ‘V’ for group Vacc1, ‘G’ for group Grau1 and ‘v’ for group Vacc2. 95% confidence interval was represented with dotted lines.