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SHORT RESEARCH NOTE

Density-dependent and inter-specific interactions affecting European eel settlement in freshwater habitats

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Abstract Identifying the factors influencing the settlement of European eel (*Anguilla anguilla*) juveniles in continental habitats is crucial to designing effective management and conservation measures for this endangered species. A long-term data series (1993–2008) of European eel and European catfish (*Silurus glanis*) abundance in a freshwater canal of the Camargue water system (southern France), along with parallel data on water salinity and glass eel abundance in the adjacent Vaccarès lagoon, was analysed to identify the possible causes of decline in eel abundance observed in the canal during the last two decades. A model including glass eel recruitment and catfish abundance as covariates explained 78% of the observed variation in eel settlement success. Results suggest that (1) salinity does not play a significant role in determining the fraction of eels moving from the brackish lagoon to the canal; (2) density dependence affects settlement success, possibly through a reduction of juvenile survival in the adjacent lagoon; and (3) catfish abundance is negatively correlated with eel settlement. We discuss this latter point in terms of possible predation of catfish upon eels and/or inter-specific competition between the two species.

Keywords *Anguilla anguilla* · Interspecific competition · Invasive species · Population dynamics · *Silurus glanis*

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Introduction

In the last few decades, European eel *Anguilla anguilla* (L.) faced a dramatic drop in recruitment, which is now down to about 1% of that observed in the 1970s (Dekker, 2003). As a result, the species was included in 2007 in the UN CITES Appendix II list and, in 2008, in the IUCN Red List as critically endangered. Conservation measures for *A. anguilla* are challenging because of the complexity of its life cycle. The European eel is a catadromous, panmictic species reproducing in the Sargasso Sea (Palm et al., 2009; Andrello et al., in press): eel larvae are carried by oceanic currents towards European and North African coasts, metamorphose into glass eels and recruit to continental waters, where they settle, feed and grow during the so-called yellow phase. When eels reach maturation size, they metamorphose into silver eels and migrate back to mating grounds, where they spawn and eventually die (Tesch, 2003). The panmictic reproduction of this species requires that conservation efforts are coordinated at the global level. In this perspective, the Council of the European Union established a framework for the recovery of the eel stock (Council Regulation 1100/2007). The Regulation requires the preparation of Eel Management Plans (EMPs) on a local scale, so as to guarantee the escapement of at least 40% of the pristine adult biomass that would be available from each river basin in the absence of anthropogenic impacts.

As global eel recruitment is presently far below pristine levels, it may be difficult to achieve the Regulation target through fishery regulation only. In fact, the reduction of fishing mortality can be effective only if a sufficient number of eels is recruited and settle in continental waters for the pre-reproductive yellow phase (Åström & Dekker, 2007). The development of a sound global conservation strategy must address a wide range of issues occurring at different spatial scales. Whilst the global amount of glass eels arriving in continental waters in a given year depends upon factors acting on a wide scale—such as the overall number of spawners reaching the reproductive grounds (Dekker, 2003), spawner quality (Geeraerts & Belpaire, 2010) and oceanic conditions (Bonhommeau et al., 2008)—both glass eel settlement in continental waters and spawner escapement are clearly affected by local environmental and biotic factors. As a consequence, a better understanding of the mechanisms influencing eel settlement in continental habitats on a local scale is crucial to devise effective management measures.

Previous studies have revealed that water salinity experienced by newly recruited eels can influence body growth rates through the lifetime (Edeline et al., 2005), and that salinity gradients amongst adjacent habitats influence eel movements according to the individual preference for brackish or freshwater habitats (Edeline et al., 2005). Demographical factors are also known to affect individual survival through density-dependent processes driven by intra-specific interactions (Bevacqua et al., 2011). In contrast, inter-specific interactions that may affect eel settlement in freshwater habitats have been usually neglected, with the exception of a recent study that found a moderate, negative impact of large colonies of cormorants upon eel survival in a French shallow lake (Carpentier et al., 2009). However, the recent introduction of invasive species may have displaced eels from the top level of the trophic chain in a number of habitats, thus requiring the reassessment of the ecological role of this species.

Invasions by non-native species have increased in the last few decades in both marine and freshwater communities, with consequences in terms of community composition and biodiversity decline (Gozlan et al., 2010). The European catfish *Silurus glanis* L. is one of the most remarkable invasive species in freshwater habitats of Western Europe. Native to Eastern Europe and Western Asia, it is the largest freshwater fish species of Europe (with adult individuals >75 kg) and has a wide piscivorous diet (Copp et al., 2009). Anecdotal evidence and grey literature suggest that European catfish introduction may be responsible for a reduction in biodiversity. As a consequence, management plans have been advocated to control and possibly limit its abundance (Puzzi et al., 2006). Yet, until now, the impact of catfish on the population dynamics of native populations has been poorly studied (Copp et al., 2009).

In the present study, we investigated the declining trend of eel settlement observed in a freshwater canal of the Camargue water system (southern France) over a 16-year period (1993–2008). Specifically, we performed a time series analysis considering glass eel recruitment, catfish abundance and water salinity as candidate explanatory variables. In fact, salinity (in the adjacent Vaccarès lagoon) and catfish abundance (within the same canal) have both been increasing during the last two decades, although with different patterns of variation, and may have influenced eel settlement in the canal.

The study area is located within the Rhône river delta (Fig. 1). It includes the Vaccarès lagoon, a brackish watershed of 6,400 ha, and the Fumemorte canal, which drains freshwater from rice fields to the lagoon. The Vaccarès lagoon has a few tributaries and is connected to the Mediterranean Sea through sluice gates located at Grau de la Fourcade. Glass eels enter into the lagoon mainly between February and

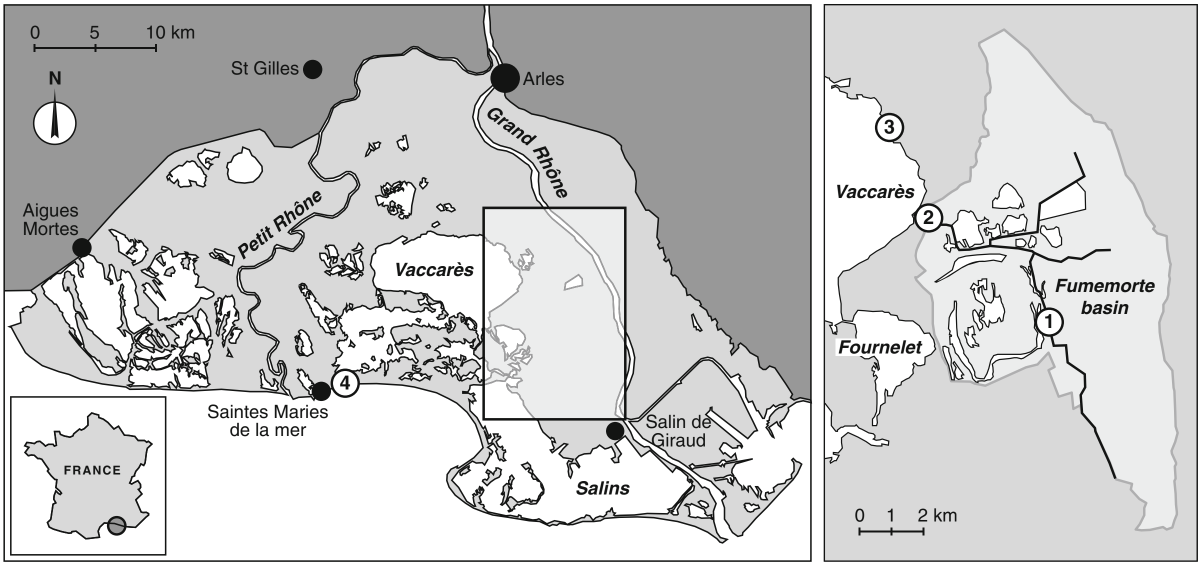


Fig. 1 The Camargue lagoons and the Fumemorte canal (*1* the sampling station at Fumemorte, *2* the dam at the outlet of the canal, *3* the sampling station at Vaccarès, *4* sluice gates at Grau de la Fourcade)

April. Most of them settle in the lagoon, while a minor fraction colonizes the adjacent freshwater canals. The Fumemorte canal is 14.6 km long and 14 m wide; its depth varies between 0.5 and 2.5 m during the year. At the outlet of the canal, a dam prevents the inflow of brackish water from the lagoon, while allowing fish to move in- and outwards. Angling (mainly with pikeperch as a target fish) is allowed only on 25% of the length of the canal; otherwise fishing is forbidden except for research purposes. European catfish were introduced in the canal at the end of the 1980s (Rosecchi et al., 1997).

Tour du Valat (TdV) biological station has been monitoring eel and catfish in the study area since 1993. Data used in this study were collected at two sites (Fig. 1), one located in the Vaccarès lagoon and one in the Fumemorte canal. In the lagoon, glass eels were sampled with two fry nets (0.5-mm mesh size) that were set in place four consecutive days per month during the recruitment peak (February to April). 3,014 glass eels were captured in Vaccarès between 1993 and 2008. The estimated annual Catch Per Unit Effort (CPUE) was then used as a proxy indicator of the abundance of glass eel recruited each year in the Vaccarès lagoon.

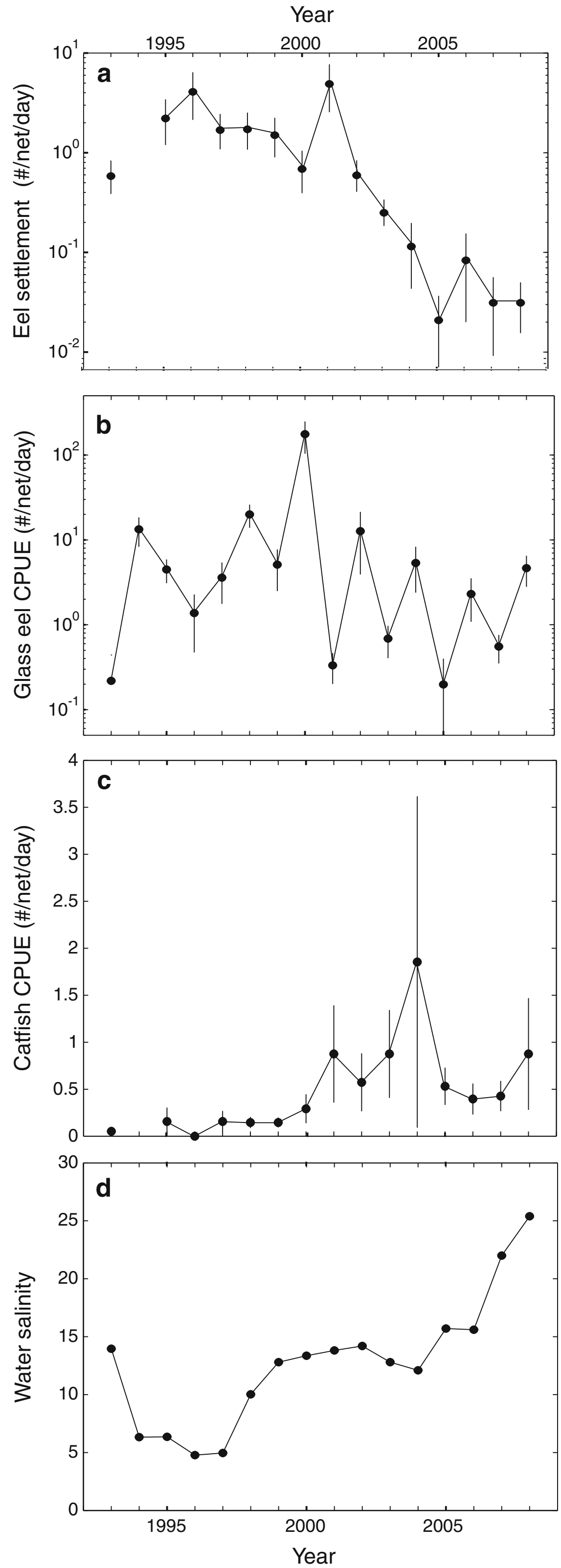
Sampling in the canal was performed with two fyke nets (6-mm mesh size) which were set in place for four consecutive days per month throughout the year. Monitoring was carried out for the first time in 1993, interrupted in 1994 and then regularly resumed from 1995 on. During the study period, 3,492 yellow eels and 759 catfish were fished in the canal. All fish were individually measured for total length (L). Annual catfish CPUE was used as a proxy of catfish abundance in the canal. Eel settlement in Fumemorte (i.e. the abundance of newly recruited eels that moved from Vaccarès to the canal) was measured as the annual CPUE of individuals with total length between 160 and 322 mm. In the following, we refer to this metric as the 'eel settlement index'. Owing to the high plasticity of body growth in eels, which has already been evidenced in the same study area (Melià et al., 2006a, b), this size range is likely to encompass 1–3-year-old individuals.

Eel settlement (E) in the canal is obviously related to glass eel recruitment to the Vaccarès lagoon (G) in the three previous years. We also assumed that settlement might be influenced by density-dependent survival of the newly recruited individuals, catfish abundance in the canal (C) and salinity (S) in the adjacent lagoon. The full model is

$$E_t = a\,\bar{G}_{t-1}\,e^{b\bar{G}_{t-1}+c\bar{C}_{t-1}+d\bar{S}_{t-1}} \quad (1)$$

where a represents the contribution of glass eel recruitment to eel settlement in the canal; b is a coefficient accounting for density dependence; c and

Fig. 2 Trend (mean ± SE) of European eel and European ▶ catfish abundance, along with water salinity, in the Camargue water system between 1993 and 2008. **a** Eel settlement index (CPUE of eels between 160 and 322 mm length) in the Fumemorte canal; **b** CPUE of glass eels recruited in the Vaccarès lagoon (February to April); **c** CPUE of catfish in the Fumemorte canal; **d** water salinity (annual mean) in the Vaccarès lagoon. (**a**) and (**b**) in log-scale



d are coefficients reflecting the effect of catfish abundance and water salinity on eel settlement, respectively; E_t is yellow eel settlement in Fumemorte in year *t*; and $\bar{G}_{t-1}$, $\bar{C}_{t-1}$ and $\bar{S}_{t-1}$ are the means of glass eel recruitment in Vaccarès, catfish abundance and salinity in the three previous years, respectively. This formulation—which is consistent with the fact that settlers in year *t* have been recruited in years $t-1$, $t-2$ and $t-3$—allowed us to considerably limit the number of candidate explanatory variables and to avoid model overparameterization. Time series of eel settlement index, glass eel and catfish abundance, and water salinity are shown in Fig. 2. To estimate the unknown parameters *a*, *b*, *c* and *d*, the model was linearized as follows:

$$\log\left(\frac{E_t}{\bar{G}_{t-1}}\right) = \log a + b\,\bar{G}_{t-1} + c\,\bar{C}_{t-1} + d\,\bar{S}_{t-1} \qquad (2)$$

The model providing the best fit to eel settlement data was selected through a backward stepwise selection procedure based on the Akaike information criterion (AIC). The best model included both glass eel recruitment and catfish abundance, while it excluded salinity as an explanatory variable ($\log a = -0.78 \pm 0.46$, $b = -0.03 \pm 0.01$, $c = -3.63 \pm 0.67$, $d =$ n.s.). This model explained 78% of the variability of the eel settlement index (Fig. 3a) and links eel settlement in the Fumemorte canal to glass eel recruitment and catfish abundance of the previous 3 years (Fig. 3b). We found no significant autocorrelation of the residuals, which would have determined the violation of the independence assumption for the error terms (Durbin-Watson statistic = 2.36, $P = 0.54$).

The remarkable changes observed in the salinity of the Vaccarès lagoon in the last years do not seem to play a significant role in explaining the decrease of eel settlement in the Fumemorte canal. Although brackish water leaking from the lagoon to the open sea was shown to act as a lure for glass eels recruitment to the Camargue water system (Crivelli

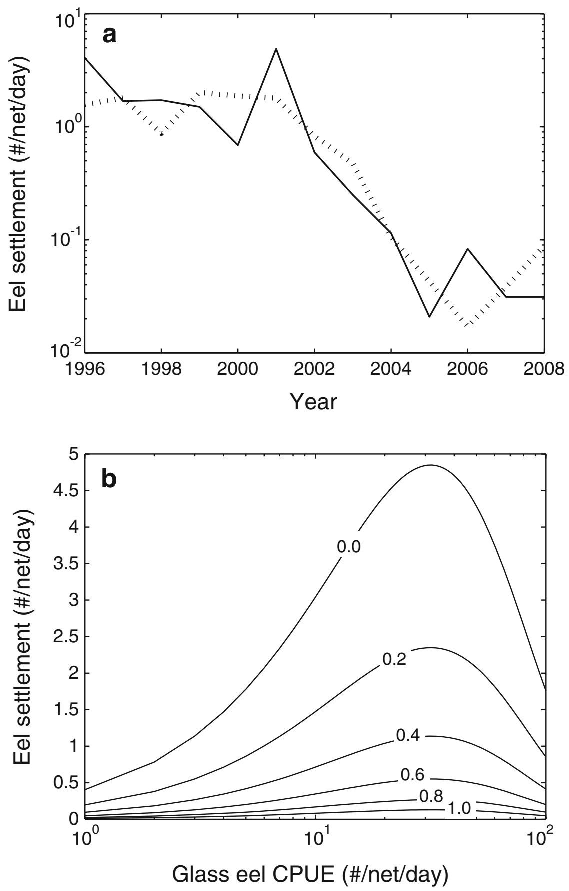


Fig. 3 Eel settlement index (CPUE of eels between 160- and 322-mm length) in the Fumemorte canal as predicted by the model. **a** Comparison between the observed (*solid line*) and predicted (*dotted line*) values in the study period (1996–2008); **b** projected values of the eel settlement index as a function of CPUE of glass eel in the Vaccarès lagoon (*x*-axis) and catfish abundance. The labels on the lines (from 0 to 1) represent increasing levels of catfish CPUE in the Fumemorte canal

et al., 2008), our results suggest that, once acclimation to the new environment has occurred in the Vaccarès lagoon, the fraction of eels migrating afterwards to the freshwater canal does not depend significantly upon lagoon salinity.

It is interesting to observe that the per-capita survival of glass eels able to settle down in the canal as 1–3-year-old yellow eels seems to decrease with increasing glass eel density in the Vaccarès lagoon. A similar conclusion about glass eel survival has been derived also in a previous study by Bevacqua et al. (2007) who calibrated a more sophisticated demographical model on data on glass eel recruitment and eel catches from Vaccarès artisanal fishery. According to our data, an exceptionally high recruitment occurred in Camargue in 2000; this event was not followed by a similarly exceptional yellow eel settlement, a fact that can be attributed to overcompensation in glass eel survival. Glass eel translocation and restocking plans are listed in the European Decision 1100/2007 as a relevant way to foster eel recovery. As a consequence, it is important to assess whether density-dependent survival from glass eel to the yellow eel stage may occur (and under which conditions) also in other water bodies. If this were the case, then it would be theoretically possible to maximize yellow eel settlement (and, in the longer run, silver eel escapement) by harvesting the newly recruited eels from sites locally experiencing high recruitment density (even temporarily) and restocking them in sites characterized by low recruitment.

The second implication of our analysis is about the interaction between European catfish and eels. This is in fact the first study documenting a negative correlation between temporal trends of these species. Obviously, a significant correlation does not imply a causative relationship between the increase of catfish abundance and eel decline. In fact, a recent review about the impact of catfish in non-native habitats seems to suggest that catfish predation may not substantially threaten native piscivorous fishes (Copp et al., 2009). However, eels have been found in the stomachs of catfish caught both in northern (Wysujack & Mehner, 2005) and southern Europe (Gualtieri et al., 2006), and small eels are the favourite bait of catfish anglers in the Rhône River (Jean-Luc Fontaine, professional fisherman on the Rhône river, pers. comm.). An alternative explanation is that catfish and eel might compete for food and/or space, as both species are predators feeding near the bottom in confined habitats. As the two explanations are not mutually exclusive, a negative impact of catfish on eels might arise from both mechanisms.

In principle, the decline of eel stocks could be due also to factors other than catfish invasion and glass eel recruitment failure, such as increasing fishing pressure, predation by piscivorous birds (such as cormorants), pollution and/or parasitic diseases. However, none of these issues is likely to play a significant role in explaining the observed decline of yellow eels in Fumemorte, professional fishing does not occur in the canal, whilst recreational fishing is strictly limited and does not target eels. Cormorants have rarely been observed in the proximity of the canal, and there exists only a small colony overwintering in the Rhône delta; in winter, eel movement is minimal because of low water temperatures, and so it is also the probability of being caught by cormorants. Despite some agricultural activities in the Camargue, average levels of organochlorine compounds in fish from this water system (both Vaccarès and Fumemorte) rank amongst the lower contamination levels reported from European coastal wetlands (Roche et al., 2000). In addition, these pollutants are unlikely to have a strong impact on eel mortality during the juvenile settlement phase (Geeraerts & Belpaire, 2010). Finally, although a remarkable fraction of the local eel stock is infected by the swimbladder nematode *Anguillicola crassus*, the infection—after a first period of increase—levelled off at the end of the 1990s (Lefebvre & Crivelli, 2004) and did not change remarkably since then; moreover, the impact on eel buoyancy of this parasite is mostly obvious in marine waters, where silver eels regularly need to dive very deep to avoid predators during their migration to the spawning areas in the Sargasso sea (Kirk, 2003; Tesch, 2003). As parasites' burden is likely to increase with age, it is unlikely that *A. crassus* can cause significant mortality in the newly recruited individuals in a shallow water canal.

The fact that *A. anguilla* has been historically considered as a dominant species in freshwater environments (Tesch, 2003) may explain why the effect of inter-specific competition with invasive fish species has traditionally gathered little attention in the literature. In the 1960s, when eels were still very abundant all over Western Europe (Moriarty & Dekker, 1997), the emphasis of scientific studies was mostly on the other way around, i.e. on the negative impact that eels could exert on other fish species such as salmonids in streams (Larsen, 1961, Sinha & Jones, 1967) and whitefish *Coregonus lavaretus* in German lakes (Herrmann, 1967). At that time, the European catfish was still confined within its native range (Copp et al., 2009) and did not pose any problem. In more recent years, the status of eel stocks has decreased so much that biological invasions may represent an additional threat to its conservation along with other known or alleged causes of eel decline. If the projections of our simple model were to be confirmed by future studies, then the geographical expansion of invasive European catfish would have become another cause for concern. Our analysis shows that the impact of catfish on eel stocks could have the potential to displace European eels from freshwater bodies. Further research on the interactions between eel and catfish is urgently needed, possibly involving stomach content and stable isotope analyses, along with culling and other manipulative experiments that test interactions other than predation. Our results suggest that management and conservation measures for European eel stocks should take into consideration ecological interactions that could jeopardize local spawner production.

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