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ORIGINAL PAPER

Biological control of invasive populations of crayfish: the European eel (*Anguilla anguilla*) as a predator of *Procambarus clarkii*

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Abstract The red swamp crayfish, *Procambarus clarkii*, is a paradigmatic invader of freshwater systems. Several attempts have been made to mitigate its multiple impacts but none was successful. Among the different methods proposed, the use of the European eel (*Anguilla anguilla*) as an indigenous predator is promising but the available information about its predatory ability on crayfish is to date scanty. To fill this gap in knowledge, we ran three experiments in wetlands and irrigation ditches in Italy. The first experiment, in the laboratory, was aimed at quantifying the extent of predation by eels on crayfish, the second, in enclosures, the size classes of crayfish mainly preyed and the possible effect of the eels on *P. clarkii* behaviour, and the third, in the field, its ability to effectively reduce crayfish populations. Results showed that eels prey on small-sized or soft crayfish, attacking them from the back; an indirect effect was to reduce crayfish trophic activity, which in turn might increases crayfish mortality due to starvation and decreases impact on the community. However, as shown in the field, the use of eels should be appropriately calibrated to the context of application. Taken together, our results show that eels might be used as a complement to the traditional trapping method. However, additional studies are necessary to understand the adequate number of eels to be introduced and to develop appropriate methods for quantifying such effects.

Keywords Invasive species · *Procambarus clarkii* · *Anguilla anguilla* · Management · Habitat conservation · Predation by fish species

Introduction

Invasive species are leading threats to biodiversity in inland waters and strongly affect the functions and services offered by freshwater ecosystems across the world (Clavero and García-Berthou 2005; Gherardi 2007). To counteract the heavy ecological and economic costs that bioinvaders inflict (Vilà et al. 2009), there is an urgent need for actions that might contain their spread and mitigate their damages. Prevention is obviously the cornerstone of management, but when invasive populations are already established in a region, control and eradication are the only available options, being most often less expensive than inaction.

Crayfish serve as keystone species in freshwater ecosystems due to their role of consumers, prey, and agents of disturbance (Momot 1995; Nyström 2002; Dorn and Wojdak 2004). Many studies have shown the ability of non-indigenous crayfish to interfere

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with native crayfish species, to reduce the biomass and richness of hydrophytes, snails, and other components of the food web, and overall to affect ecosystem services (e.g. Lodge et al. 1994; Nyström et al. 1996; Gherardi and Acquistapace 2007; Gherardi 2007). A paradigm of invasive crayfish is the red swamp crayfish *Procambarus clarkii*, a species native to north-eastern Mexico and south-central USA (Hobbs 1989) and now abundantly diffused across the world (Gherardi 2006). As with some other crayfish species, *P. clarkii*, once introduced for stocking and aquaculture and kept in outdoor ponds, almost inevitably escapes and easily establishes self-sustaining populations in the colonized habitats. Due to its ability to travel long distances even overland, this species has spread widely from the point of introduction, becoming invasive in nearly all of areas where it has been introduced.

A number of interventions that attempted to restore the populations of predatory fish have shown to be effective in reducing the size of the invasive crayfish populations, particularly if accompanied by intensive trapping (e.g. in Sparkling Lake, USA; Hein et al. 2007). Among the fish species native to Europe, the eel *Anguilla anguilla* might be a predator of *P. clarkii* because of its benthonic feeding habit and ability to tolerate partially deoxygenated waters, properties that match the lifestyle of crayfish and the typical habitats they occupy. If compared to other more active fish species, eels are expected to be even more efficient as predators because they are able to detect crayfish by odour (Blake and Hart 1995a). Except for some anecdotal reports (Frutiger and Müller 2002), however, no experimental studies have ever attempted to explore their effective predator efficiency on *P. clarkii*.

This study aims at testing the potential use of the European eel for the control of invasive populations of *P. clarkii* by analyzing the number and size of the crayfish preyed upon and eels' catching ability. We also investigated whether eels exhibit some indirect effects on crayfish by, for example, inducing a change in their behaviour, as previously suggested for other fish species (Stein and Magnuson 1976; Stein 1977; Blake and Hart 1993). To achieve these aims, three experiments were carried out. First we quantified the predatory efficacy of eels in the laboratory; then, in an enclosure experiment, we determined the size of the most preyed crayfish and the effect of the eels on crayfish behaviour; finally, we investigated their effective ability to reduce natural crayfish populations.

Materials and methods

Experiment 1

Fifteen adult eels (total body length: 41 ± 1.5 cm) and 300 *P. clarkii* males (cephalothorax length: 14.1–64.2 mm) were fished using baited traps in June 2006 from the Nature Reserve of ''Padule di Fucecchio'' (43°48′0″N, 10°47′38″E; 13–16 m a.s.l.) (Tuscany, Italy). In the laboratory, eels and crayfish were maintained at natural light:dark cycle and air temperature of 20°C. Eels were kept for 3 weeks in acclimation aquaria (diameter: 200 cm) with circulating water and fed every 2 days with dead crayfish. The total length of each eel was measured with a rule. Crayfish were kept at a density of 15 m^{-2} in plastic tanks (80 × 60 × 60 cm) containing 48 L of circulating water and halved terracotta pots as shelters. They were fed ad libitum with live *Calliphora* sp larvae. Only hard-shelled males with all appendages intact were used in this experiment. For each experimental crayfish, we measured the weight three times using an electronic scale (ORMA Model BC 250, accuracy 0.001 g) and the length of the cephalothorax (CL), from the tip of the rostrum to the posterior edge of the carapace, using a vernier caliper (to the nearest 0.1 mm). Each individual was marked with a waterproof paint.

Experiments were conducted from July to September 2006 in four circular plastic tanks (diameter: 100 cm, water depth 30 cm). Two air stones and an air-driven sponge filter provided circulation and aeration in the experimental tanks. We placed four groups of two 15–20 cm flat rocks in each tank to offer shelter to crayfish. In the treatment (5 replicates per size class), we used an eel and 10 crayfish belonging to the same size class, i.e. small (CL < 25 mm), medium (CL: 25–40 mm), and large (CL: >40 mm). Size classes were established on the basis of the size distribution of the captured crayfish. Simultaneously, we ran 5 replicates per size class as control, in which crayfish were kept in the same conditions as the treatment but without eels. Each trial lasted 14 days, during which, once per day at 12.00, we recorded: (1) the number and weight of the crayfish preyed upon, (2) the number of exuviae left in the pool, and (3) the crayfish body parts most often consumed. After our check, dead crayfish were replaced with live individuals of the same size class. At the end of each trial, the experimental tanks were emptied and thoroughly washed with tap water.

Experiment 2

The experiment was conducted in May–August 2007 in the wet area “Righetti-La Monaca” in the Nature Reserve of “Padule di Fucecchio”. In this area, the density of European eel has dramatically decreased (50% decrease in 20 years). On the contrary, *P. clarkii*, first recorded in the area in 1996 (Bartolini 2007), reaches now a density of 14 m^{-2} (Scalici and Gherardi 2007); its impact on the biomass of the community and on the richness of indigenous species has been found to be extremely strong (Gherardi and Acquistapace 2007).

A total of 11 adult eels and 500 hard-shelled Form I crayfish males with all appendages intact were captured using baited traps in the area. Crayfish were individually marked and measured as in Experiment 1. Along a 300-m canal, 23 cages (50 × 50 × 200 cm; wide mesh: 2 mm) were installed at a distance of 3 m from each another. Each cage was enriched with hydrophytes to increase habitat complexity and with 15 clay pots (5 cm in diameter) as shelter, whereas macro-invertebrates were free to enter. Fifteen crayfish of three size classes, defined on the basis of the size distribution of the captured crayfish: 5 small ($CL < 40$ mm) 5 medium (CL: 40–50 mm), and 5 large (CL: > 50 mm) were inserted into each cage, reaching a density (15 m^{-2}) corresponding to the natural one (Scalici and Gherardi 2007). In each treatment cage (11 out of 23), an adult eel (total body length: 46 ± 1.8 cm) was added. Experiments lasted for 20 days. Cages were inspected every week, and the number of dead crayfish and their size were noted. Each dead crayfish was replaced with a live one of the same size class. At the end of the experiment, the surviving crayfish were collected and frozen. Their gut was then analyzed for their content. Following Gherardi and Barbaresi (2008), three food categories were distinguished (vegetal items, animal remains, and inorganic sediments) and an index of gut fullness was estimated by sight, assigning to each gut one of four scores (1: 0–25%; 2: 25–50%; 3: 50–75%; and 4: 75–100%).

Experiment 3

The experiment was carried out from July to September 2008 in two artificial canals (Mandriolo and La Pia) located in the “Consorzio di Bonifica Parmigiana Moglia-Secchia” (44°46′14″N; 10°46′59″E, 25–58 m above the sea level) (Emilia–Romagna). *P. clarkii*, first recorded in the area in 1998, has now an extremely high density (20 m^{-2}) (Sala et al. 2000), whereas the abundance of the eel has sharp decreased.

Two 150 m-long transects (3 m width) per canal, with similar environmental characteristics, were delimited using 2 mm-mesh wire netting. One transect per canal was randomly assigned to the treatment (T), which consisted of introducing 15 adult eels after 1 week from the start of the experiment, whereas the other transect was the control (C).

The experiment was planned in three phases. In phase 1, lasting 1 week, the density of the crayfish population was estimated using the Catch per unit Effort (CPUE) method (see below). At the end of phase 1, 15 adult eels (mean length: 52 ± 8.36 cm; mean weight: 179.62 ± 37.16 g) were introduced into each of the T transects. Phase 2 followed the introduction of eels and lasted 2 weeks. During this phase, we estimated the short-term effect of the eels on crayfish. Their long-term effect was assessed in Phase 3, lasting 1 week, which was conducted 1 month after the end of Phase 2.

In the three phases, crayfish were intensively trapped, using six baited traps for each transect, and removed from the area. Catch rate was expressed as Catch per unit Effort (CPUE), i.e. the number of crayfish per trap per 24-h period (crayfish $trap^{-1}$ - day^{-1}). To estimate possible differences between the diurnal and nocturnal activity of crayfish, traps were emptied twice a day, i.e. at sunrise (at 07:00 h) and at sunset (at 20:00 h). For each crayfish, sex and CL were determined, as in Experiments 1 and 2. The number of the females with pleopodal eggs was also recorded.

Statistical analysis

Data were first tested for normality and homogeneity of variance after the Kolmogorov–Smirnov and Levene test, respectively, which allowed us to use parametric tests when appropriate (Sokal and Rohlf 1969). General Linear Models for repeated measures (GLMs, statistic: *F*), followed by Tukey *post hoc* tests, were used to compare mortality between control and treatment cages and CPUE between control and treatment transects; the number of dead crayfish per size class and the CPUE values were the within-subjects factors, respectively, and the treatments (with or without eels) were the between-subjects factors. Student's *t*-tests (statistic: *t*) were used to compare CL between preyed and not preyed crayfish (two-tailed for independent samples). Relationships between the eel size and the number of preyed crayfish were analyzed with Pearson correlation tests (statistic: r^2). The non-parametric *G* test with Williams' correction (statistic: *G*) was used for frequency data. The level of significance under witch the null hypothesis was rejected is $\alpha = 0.05$. Text gives mean values ± SE.

Results

Experiment 1

Survival rate differed between the control and the treatment ($F = 9.083, df = 1, P = 0.006$), indicating, as expected, that eels effectively prey on crayfish. Predation rate was similar among crayfish size classes ($F = 0.015$, $df = 2$, $P = 0.985$). However, predation on the largest crayfish was associated with the constant presence of exuviae, leading us to believe that the eel preferentially preyed upon large individuals when soft. The number of dead crayfish in each size class also increased with the number of exuviae in the treatment tanks ($r^2 = 0.913$, $t = 4.838$, $df = 10$, $P = 0.0001$), whereas such a significant correlation disappeared in the control tanks ($r^2 = 0.320$, $t = 1.160$, $df = 10$, $P = 0.274$), again suggesting that predation is always stronger on moulting crayfish. Daily consumption of crayfish was 1.33% of eel weight independently of the crayfish size ($F = 1.877$, $df = 2$, 15, $P = 0.195$). Crayfish remains indicated that eels attacked hard shelled crayfish at the back starting to eat it from the telson and avoiding their chelipeds. Both carapace and chelipeds were not generally consumed in individuals with CL > 40 mm.

Experiment 2

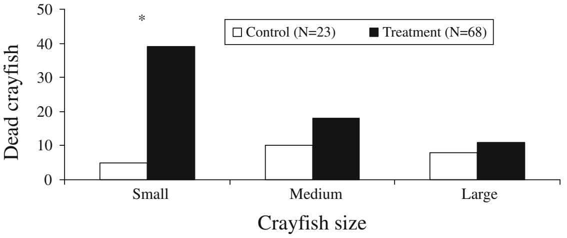

Fig. 1 Experiment 2: number of crayfish per size class found dead or missing in the control (without eel, $N = 23$) and in treatment (with eel, $N = 68$). The asterisk denotes significant differences at $P < 0.001$ after Mann–Whitney tests

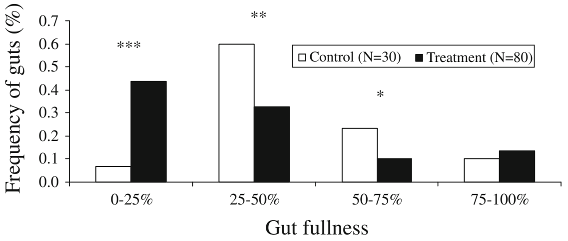

Fig. 2 Experiment 2: frequency of guts in four classes of fullness compared between control (without eel, $N = 30$) and treatment (with eel, $N = 80$). *, **, and *** denote significant differences at $P < 0.05$, 0.01, and 0.001, respectively, after *G*-tests with William's correction

As expected, crayfish mortality was significantly higher in the treatment than in the control cages ($G = 23.135$, $df = 1$, $P < 0.001$). The mean size of the preyed crayfish (39.27 ± 1.04 mm) significantly differed from the mean size of the crayfish survivors (45.07 ± 0.5 mm; $t = 4.707$, $df = 217$, $P = 0$), which means that the predatory efficiency is highest towards small individuals. Accordingly, preyed crayfish generally belong to the small size class ($F = 10.589$, $df = 2$, $P = 0$, Fig. 1). Number ($r^2 = 0.245$, $t = 1.707$, $df = 10$, $P = 0.122$) and size ($r^2 = 0.253$, $t = 1.747$, $df = 10$, $P = 0.115$) of the preyed crayfish showed a tendency to increase with the size of the predator. As it seems clear from the analysis of gut fullness, crayfish significantly reduced their trophic activity in the presence of the eel, probably due to the increased time spent in shelter to avoid predation (Fig. 2).

Experiment 3

The two experimental canals significantly differed for the total number of the crayfish trapped ($G = 3{,}249.886$, $df = 1$, $P < 0.001$) with a total of 2,959 and 9,065 individuals removed in La Pia and

Mandriolo, respectively. The different CPUE between the two canals ($t = -6.193$, $df = 97$, $P = 0$) seems to suggest an original difference in population sizes. No difference was found in the CPUE at sunrise and at sunset (La Pia: $t = 0.224$, $df = 50$, $P = 0.824$; Mandriolo: $t = 0.284$, $df = 45$, $P = 0.778$). Catch rates declined during the phases 1 and 2 in La Pia ($r^2 = 0.237$, $t = -5.235$, $df = 89$, $P = 0$), whereas it was constant in Mandriolo ($r^2 = 0.012$, $t = -0.988$, $df = 81$, $P = 0.326$). However, no difference was found between T and C transects in either canal (La Pia: $F = 3.314$, $df = 1$, $P = 0.073$; Mandriolo: $F = 0.140$, $df = 1$, $P = 0.710$) (Fig. 3). In the absence of trapping for a month, the number of crayfish increased in La Pia ($F = 93.848$, $df = 1$, $P = 0$), reaching values comparable to those found at the beginning of the study, but decreased again during phase 3 ($r^2 = 0.477$, $t = -3.308$, $df = 13$, $P = 0.006$). Sex ratio significantly differed between canals ($G = 1{,}359.656$, $df = 1$, $P < 0.001$), reaching 32% in La Pia and only 1.8% in Mandriolo. However, no difference was found between T and C transects ($G = 0.782$, $df = 1$, $P > 0.05$). The numbers of reproductive females (La Pia: 16 out of 356; Mandriolo: 5 out of 723; $G = 0.807$, $df = 1$, $P > 0.05$) and of pleopodal eggs were significantly correlated to the female size ($r^2 = 0.693$, $t = 3.003$, $df = 5$, $P = 0.04$), being however independent of the treatment/control ($G = 0.365$, $df = 1$, $P > 0.05$).

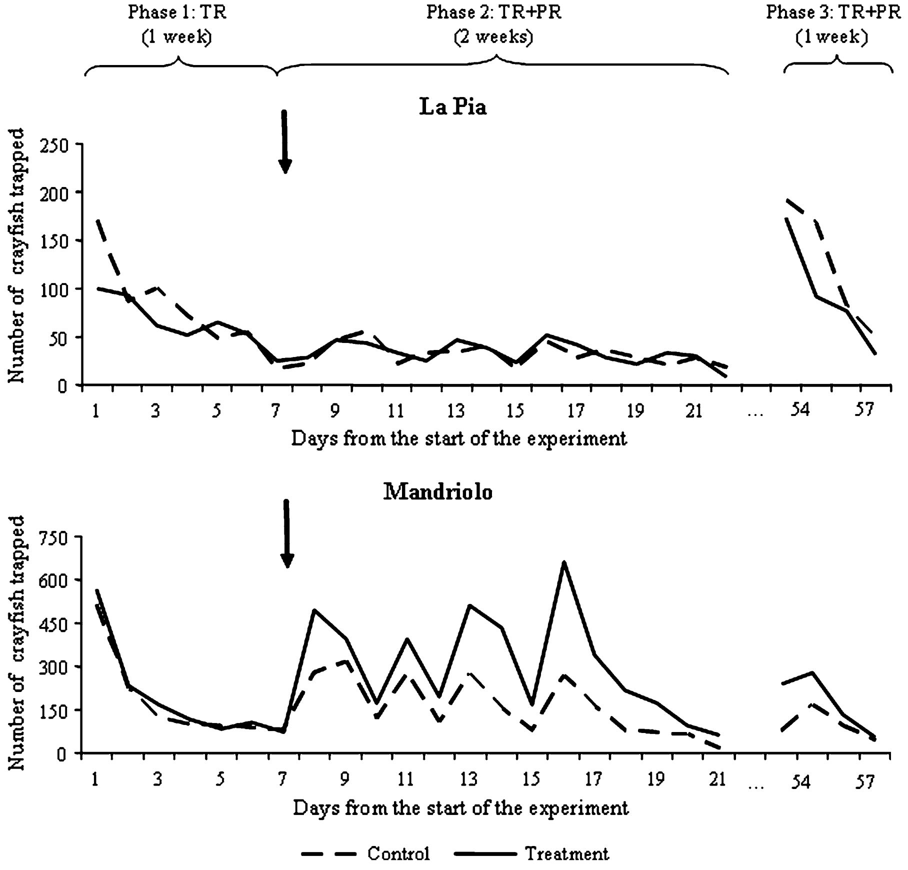

Fig. 3 Experiment 3: mean daily number of *Procambarus clarkii* trapped in the control (*broken line*) and treatment (*continuous line*) transects in two artificial canals (La Pia, *top*, and Mandriolo, *bottom*). The *arrow* indicates the introduction of eels. *Brackets* denote the three phases of the study, i.e. phase 1 (1 week): crayfish were subject to trapping only, TR; phase 2 (2 weeks), after the introduction of eels: crayfish in the treatment transects were subject to both TR and eels' predation, PR; and phase 3 (1 week), after 1 month without trapping: crayfish in the treatment transects were again subject to TR and PR combined. In the three phases, crayfish in the control transects were subject to TR only

Discussions and conclusions

Taken together, our results confirm that *P. clarkii* is vulnerable to *A. anguilla* as a predator and indicate that fish predation combined with trapping might be effective in controlling invasive populations of crayfish, at least, in enclosed areas where fish dispersion might be avoided. However, the present study also suggests that the two methods should be appropriately calibrated to the context of application.

As expected from previous studies (Svärdson 1972; Frutiger and Müller 2002), eels are efficient predators of *P. clarkii*. Similarly to other fishes such as smallmouth bass and rock bass (Hein et al. 2006), eels are gape-size limited, mostly preying on small crayfish. The limited susceptibility of large crayfish to eel predation may be due to a number of reasons. First, large-sized crayfish have also big and dangerous chelae: our laboratory experiment showed that eels usually avoid larger crayfish and always attack the smaller from behind. Second, large crayfish are the winners of intraspecific fights for the access of shelters (Stein and Magnuson 1976; Capelli and Munjal 1982); since appropriate shelters are often limited in the habitat, the less-competitive small individuals may thus suffer higher rates of predation (Butler and Stein 1985; Garvey et al. 1994). Finally, adult crayfish might recognize, more easily than small individuals, eels as predators, even though they have never had experience with them, and may display an efficient anti-predatory behaviour, such as sheltering. Indeed, in the presence of odours from food deprived eels, predator-naïve juveniles of another invasive species, *Pacifastacus leniusculus*, were found to reduce the use of shelters and to increase their foraging activity, whereas an opposite response was shown by juveniles of the native *Astacus astacus*, a species that has a long co-evolutionary history with eels in Finland, where this experiment was done (Hirvonen et al. 2007). On the contrary, as shown by Hazlett et al. (2002), adults of *P. clarkii* are able to associate the odour of a novel fish species even if herbivorous, e.g. the goldfish, with the alarm odours released by conspecifics and display anti-predatory behaviours.

However, the gape-size limited predatory behaviour of fish can be compensated by intensive trapping. Smaller individuals, in fact, are usually trap-shy, whereas traps mostly attract large, usually male reproductive crayfish (Aquiloni and Gherardi 2008). This confirms the need to include complementary methods, e.g. trapping, for the control of invasive populations of *P. clarkii* and of other crayfish, as also suggested by Hein et al. (2006).

Fish may contribute to the mortality of adult crayfish if soft-shelled, as shown in our laboratory experiment (see also Behrendt 1987). There are in fact some records of the habit of *P. clarkii* to moult in the open, even in the presence of predators; possibly to reduce the risk of being cannibalized inside communal burrows (Hartmann and O'Neill 1999).

Fish predators may also modify the behaviour of crayfish, inducing the reduction of their activity or a shift in its peak and an increase in the time spent in shelter (Stein and Magnuson 1976; Stein 1977; Hamrin 1987; Blake and Hart 1993, 1995a, b). This indirect effect of eels was confirmed by our analyses of the content of crayfish guts: the reduced activity of *P. clarkii* in the presence of eels translates into its decreased trophic activity. As a consequence, the limited foraging we recorded might lead to an increased mortality of crayfish due to starvation, on one hand, and to a decreased impact on the most affected components of the community such as macrophytes and snails, on the other.

Notwithstanding the above listed encouraging results, our study also highlights some aspects that should be taken into due consideration before applying the method at large scale. First, *A. anguilla* seems not to be as voracious as other fish species used for control purposes (e.g. *Micropterus salmoides*, Rach and Bills 1989; *Esox lucius*, Elvira et al. 1996). Experiment 1, in fact, showed that eels consume a small number of crayfish amounting to ca. 1 crayfish every 4 days, i.e. 1.33% of the eel weight. If, on one hand, our results may be biased by the stress inflicted on eels by their confinement in a tank; however, the consumption we recorded is comparable with what has been found in aquaculture (Owen et al. 1998) and may be ascribed to the lower metabolic rate of eels with respect to other fish species (Owen 2001). As a consequence, to balance the limited food requirement of *A. anguilla*, a large number of fish should be used. It is, in fact, the small number of the eels introduced (1 individual every 30 m^2) that might explain the negative results of Experiment 3. In this field experiment, in fact, no difference in CPUE between the treatment and the control transects was found and none of the other parameters analysed (diurnal/nocturnal activity, sex ratio and number of reproductive female) showed any apparent change due to the eels' predation. On the contrary, the recorded reduction of captures with time seems to be only ascribed to the intensity of trapping. In fact, when trapping was suspended for a month, crayfish populations increased again, at least in a canal. A second pitfall of this field experiment lies in using the number of trapped crayfish to estimate short-range changes in population size; with this method we were in fact able to assess the abundance of large crayfish and not the abundance of small individuals on which predation is more effective, because more trap-shy.

The second issue to consider is that *A. anguilla* stocks in Europe are in rapid decline because of overfishing, pollution, and habitat destruction (Moriarty and Dekker 1997; Dekker 2000). The European Commission, the International Council for the Exploration of the Sea (ICES), and the European Inland Fisheries Advisory Commission (EIFAC) have all advised that urgent management action needs to be taken to protect and restore eel stocks (see Council Regulation EC n.1100/2007). Following these recommendations, the introduction of eels for the control of invasive crayfish populations should be preceded by a series of integrated actions aimed at restoring suitable habitats for the species and regulating its fishing. This would lead to increased efforts in terms of costs and time.

In conclusion, although our results foster hopes in the struggle against invasive crayfish, showing the potential of *A. anguilla* to be used as an efficient predator of *P. clarkii* with the important additional benefit to promote this threatened fish species' conservation, additional field studies are required to understand the adequate number of eels to be introduced in order to get substantial effects on crayfish populations and to develop appropriate methods for quantifying such effects.

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