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The influence of the invasive black bullhead *Ameiurus melas* on the predatory efficiency of pike *Esox lucius* L.

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The influence of the invasive black bullhead *Ameiurus melas* on the predatory efficiency of the pike *Esox lucius* was investigated using an additive experimental design. Pike predatory success on 0+ years roach *Rutilus rutilus* was significantly reduced in the presence of black bullhead. Among the different hypotheses that may explain such a pattern, the hypothesis of direct competition between pike and black bullhead was not verified, as black bullhead hardly fed on roach. Similarly, pike predatory efficiency did not decrease with turbidity, rejecting therefore the hypothesis of an indirect effect through black bullhead-generated turbidity. Therefore, the reduced predatory efficiency of pike was probably related to behavioural interference between pike and black bullhead. These laboratory results confirm the potential negative impact of black bullhead on native European fauna, with a particular emphasis on pike, which is a top predator considered as vulnerable in some European regions.

Key words: invasive species; multipredator; predatory efficiency; turbidity.

INTRODUCTION

Freshwater ecosystems have received many fish invaders (Welcomme, 1988; Leprieur *et al.*, 2008*a*), and these invasive species have been recognized as a major threat to biodiversity and ecosystem integrity (Vitousek *et al.*, 1997; Mack *et al.*, 2000). Non-native fishes can modify the strength of biotic interactions (competition and predation) within native communities (Townsend, 2003; Blanchet *et al.*, 2007). They can also play a role in the introduction of parasites and diseases, contribute to genetic deterioration and modify the environment (Taylor *et al.*, 1984). According to Holčík (1991), 134 non-native freshwater fishes have been introduced in Europe and almost all large European river basins are now invaded by non-native species (Clavero & Garcia Berthou, 2006; Leprieur *et al.*, 2008*b*). The effect of most fish introductions on the native European fish fauna, however, is still unknown (Elvira, 2001).

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The black bullhead *Ameiurus melas* (Rafinesque) an ictalurid fish native to North America, is one of the most abundant non-native fish species in European freshwater ecosystems (Declerck *et al.*, 2002; Cucherousset *et al.*, 2006). Black bullhead can account for >30% of fish abundance (Boët, 1980; Cucherousset *et al.*, 2006), with biomasses ranging from 5 to 50 kg ha^{-1} (Louette & Declerck, 2006). Most European policies therefore consider this species as liable to cause biological disequilibrium (Elvira, 2001; Keith & Allardi, 2001).

The black bullhead is a benthivorous fish inhabiting standing waters with soft bottom substrata (Keith & Allardi, 2001), and its activity is known to generate turbidity (Braig & Johnson, 2003). Although usually considered as detritivorous, its diet may include live fishes (Boët, 1980). Black bullhead may therefore affect the native fauna in three distinct ways. First, it may prey directly on some species, therefore reducing the amount of available prey for native predators. Second, black bullhead may have an indirect effect by generating turbidity (Braig & Johnson, 2003), that can modify the feeding efficiency of visual predators (Reid *et al.*, 1999; Utne-Palm, 2002). Third, due to their high local abundance, black bullhead behaviour may interfere with accompanying species and hence negatively affect the behavioural feeding phases of native predators and the anti-predator behaviour of native prey.

In this context, the direct (*i.e.* predation), indirect (*i.e.* turbidity) and interference effects of black bullhead on the predatory efficiency of pike *Esox lucius* L. were examined in the laboratory; more specifically whether black bullhead in the presence of pike led to a predation risk reduction or enhancement for prey in clear and turbid waters. The pike was selected as it frequently co-occurs with black bullhead in Europe (Cucherousset *et al.*, 2007). Moreover, the two species commonly prey on roach *Rutilus rutilus* (L.) (Boët, 1980; Hart & Connellan, 1984) and may therefore compete for food. In addition, pike is a visual predator (Casselman & Lewis, 1996) that may be affected by the turbidity generated by black bullhead activity. In the present study, an additive experimental design (Griffen, 2006) was conducted at two turbidity levels (*i.e.* clear and turbid water), which consisted of comparing predation by each species separately to predation when the species were combined. This design is commonly employed to detect predation risk reduction or enhancement for prey subject to consumption by multiple predators (Sih *et al.*, 1998).

MATERIALS AND METHODS

EXPERIMENTAL DESIGN

Experiments were carried out in autumn 2006. Wild fishes were used exclusively to avoid potential bias due to behavioural changes between farmed and wild strains (Johnsson *et al.*, 2001). Black bullhead and pike were 1+ year fishes, 143·1 ± 1·1 mm total length (L_T) and 30·2 ± 0·7 g and 267·4 ± 4·0 mm L_T and 77·9 ± 5·6 g (mean ± S.E.), respectively. Roach 0+ years old were selected as they are a prey for pike and black bullhead in Europe (Boët, 1980; Bruslé & Quignard, 2001). The L_T and mass of roach (83·0 ± 0·8 mm L_T and 4·2 ± 0·1 g) were consistent with those found in the stomach content of both pike and black bullhead (Hart & Connellan, 1984; Declerck *et al.*, 2002). Prior to the experiments, each species was kept for 2–6 weeks in separate 600 l tanks. Roach were fed with fish pellets, black bullhead with 0+ year roach and fish pellets and pike with 0+ year roach. Pike and black bullhead were starved for a week before the start of each experiment.

Experiments took place in 200 l tanks (1000 × 400 × 500 mm) at a temperature of 18 ± 0·5° C, range. The bottom of each tank was filled with 50 mm fine sandy substratum (grain size <1 mm). Diffuse light conditions (1600 lx, range ±10 lx) were provided by four fluorescent tubes mounted 150 mm above the tank, which reproduced sunlight with a natural photoperiod (light was automatically turned on at dawn and off at dusk). The additive experimental design consisted of one control treatment (no-predators) and three predator treatments: pike-alone, black bullhead-alone and the two predators together. The prey density was identical in each treatment (10 0+ year roach): (1) 10 roach were introduced in the control treatment, (2) one pike and 10 roach in the pike treatment, (3) three black bullheads and 10 roach in the black bullhead treatment and (4) one pike, three black bullheads and 10 roach in the multipredator treatment. Introducing three black bullheads per tank gave a similar predator biomass in the pike and black bullhead treatments and recognized the gregarious habits of this species (Bruslé & Quignard, 2001; Keith & Allardi, 2001). Likewise, introducing no more than one pike per tank is consistent with the territorial habits of this species (Eklöv & Hamrin, 1989).

Each treatment was run at two turbidity levels: low turbidity, clear water (CW, 1·5 ± 0·04 nephelometric turbidity units, NTU, mean ± S.E.), and high turbidity, turbid water (TW, 72·5 ± 0·3 NTU). Turbidity was stabilized using an aquarium water pump. It was measured five times a day with a Hach 2100P portable turbidimeter (Hach Company, Loveland, CO, U.S.A.) that quantifies the amount of light from an incandescent bulb, scattered at a 90° angle, in NTU. In TW experiments turbidity was controlled by adding 40 g of bentonite clay to the experimental tanks. The TW turbidity was *c.* 70 NTU, a level frequently observed in stagnant lowland water bodies invaded by black bullhead (*e.g.* dyked wetlands; Braig & Johnson, 2003).

Before each experiment (in both CW and TW experiments), fishes were acclimated for 12 h. During this period, tanks were separated into two equal parts by a plexiglas sheet to keep predators away from prey. The separation was carefully removed at the end of the acclimatizing period. Each experiment lasted 3 days (72 h). At the end of each experiment, the number of remaining roach was counted to deduce the predatory efficiency of each single predator. In the multipredator treatment, only black bullheads were killed and their stomach contents were analysed since pike is classified as vulnerable in France (Keith & Allardi, 2001). The number of remaining roach was also counted at the end of the experiment. This allowed the number of roach consumed by black bullheads and by pike to be determined. At the end of each experiment, all the fishes were removed from the tank and a new set of fishes were used for the following replicate to avoid pseudoreplication. Between each replicate, the tank was emptied and the water was changed to avoid potential bias due to chemical cues. All experiments were replicated eight times. All the pikes were released after the experiments in the same area they were caught.

DATA ANALYSIS

The multiple predator effect was determined by comparing the number of prey remaining for the four treatments (*i.e.* pike, black bullhead, pike and black bullhead, and no-predator control) at two turbidity levels. To do this, a three-way ANOVA was applied on ln-transformed prey abundance at the end of each experiment, with the presence or absence of each predator species treated as a separate factor (Sih *et al.*, 1998; Griffen, 2006). A significant two-way interaction (pike × black bullhead) indicates the presence of a non-additive effect of combining the two predator species and significant three-way interaction (pike × black bullhead × turbidity) indicates that the effect of the two predators changes with turbidity. Then, the predator efficiencies of pike and black bullhead at two turbidity levels were compared using two-way ANOVA on ln-transformed number of prey consumed. Multiple *post hoc* comparisons were conducted with Tukey's HSD tests. Data were ln-transformed prior to each analysis to meet the assumptions for parametric statistical analysis (*i.e.* normality and homoscedasticity).

RESULTS

The number of roach remaining for each treatment revealed that turbidity did not affect prey vulnerability (Table I). Then, a lower number of remaining prey was found in the pike-alone treatment than both in the no-predator control (Tukey's test, $P < 0{\cdot}001$; Fig. 1) and in the black bullhead-alone treatment (Tukey's test, $P < 0{\cdot}001$; Fig. 1). In contrast, the number of remaining prey when pike and black bullhead were combined was greater than expected by the additive experimental design (significant pike × black bullhead interaction; Table I). The number of remaining prey in the multipredator treatment was significantly greater than in the pike-alone treatment (Tukey's test, $P < 0{\cdot}05$; Fig. 1), but did not significantly differ from that observed in both the no-predator treatment (Tukey's test, $P > 0{\cdot}05$; Fig. 1) and the black bullhead-alone treatment (Tukey's test, $P > 0{\cdot}05$; Fig. 1). Last, the number of prey remaining in the black bullhead-alone treatment did not differ from that observed in the no-predator control (Tukey's test, $P > 0{\cdot}05$; Fig. 1).

Considering the number of roach consumed by each predator revealed consistent results (Table II). Moreover, a significant effect of black bullhead on the predation efficiency of pike was found (Table II), resulting in a significant decrease in the number of roach consumed [Tukey's test, $P < 0{\cdot}01$; Fig. 2(a)]. In contrast, pike did not affect the roach consumption by black bullhead [Table II and Fig. 2(b)]. Last, turbidity did not affect the predatory efficiency of either pike or black bullhead (Table II).

DISCUSSION

In this study, the effect of a turbidity level (*c.* 70 NTU) frequently observed in standing waters invaded by black bullhead (Braig & Johnson, 2003) was tested on the predator efficiency of pike. The predatory success of pike was not affected by turbidity. This result contrasts with previous studies that showed that turbidity reduced the feeding efficiency of visual predators such as *Micropterus salmoides* (Lacepède, 1802) (Reid *et al.*, 1999) and *Perca fluviatilis* L., 1758 (Pekcan-Hekim & Lappalainen, 2006). These results, however, parallel those of Mauck & Coble (1971) on the independence between pike feeding efficiency and water turbidity. Although the ability to detect prey by

TABLE I. Three-way ANOVA applied to compare the number of remaining prey in the multiple and single predator treatments at two levels of turbidity (clear water or turbid water)

Source of variation	d.f.	SS	*F*	*P*
Pike	1	3·685	21·206	0·000
Black bullhead	1	0·653	3·758	0·058
Turbidity	1	0·069	0·394	0·533
Pike × black bullhead	1	0·970	5·583	0·022
Pike × turbidity	1	0·127	0·728	0·397
Black bullhead × turbidity	1	0·003	0·018	0·894
Pike × black bullhead × turbidity	1	0·019	0·109	0·743
Error	56	9·730		

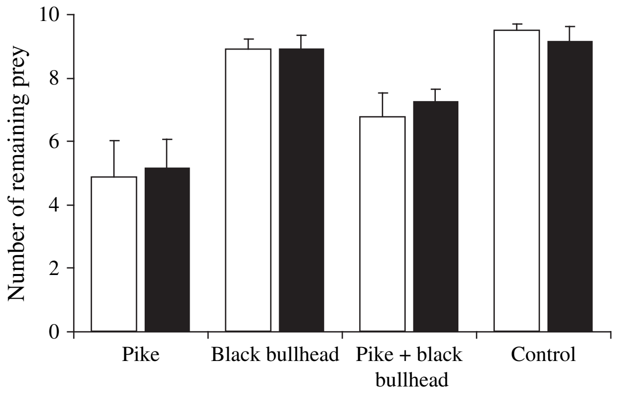

FIG. 1. Mean + S.E. number of remaining prey ($n = 8$) in each experiment for clear (□) and turbid (■) water conditions.

visual predators, such as pike, is probably affected by turbidity, this may be compensated by an equivalent decrease of prey ability to detect predators (Gregory, 1993).

Whatever the turbidity level, no significant effect of multiple predator treatment on the number of remaining prey compared to no-predator control was observed. In other words, pike predatory efficiency was significantly reduced by the presence of black bullhead. Three main processes can account for this decrease in pike predation efficiency: (1) direct competition between pike and black bullhead for roach prey, (2) an interaction other than competition between roach and black bullhead interfering with pike foraging success and (3) an interaction between pike and black bullhead reducing pike foraging success.

A direct competition between pike and black bullhead for roach prey is unlikely as the number of prey consumed by black bullhead did not differ from the mortality of roach in the absence of any predator. This means that black bullhead fed little on roach in the experiments. Although black bullhead is considered as an opportunistic predator (Businessé & Quignard, 2001), able to prey

TABLE II. Two-way ANOVA of roach prey consumption by single predators in the presence of another predator at two turbidity levels (clear water or turbid water)

Source of variation	d.f.	SS	*F*	*P*
Pike predation efficiency	1			
Black bullhead	1	2·791	12·986	0·001
Turbidity	1	0·006	0·029	0·865
Black bullhead × turbidity	1	0·000	0·001	0·971
Error	28	6·017		
Black bullhead predation efficiency	1			
Pike	1	0·212	0·902	0·350
Turbidity	1	0·013	0·055	0·817
Pike × turbidity	1	0·001	0·004	0·951
Error	28	6·571		

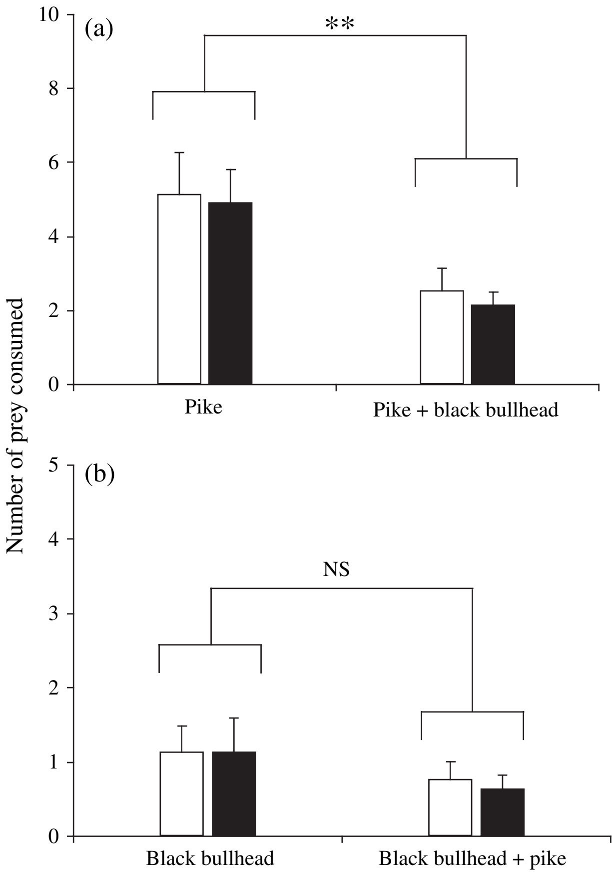

FIG. 2. Mean + S.E. number of prey ($n = 8$) consumed by each predator in clear (□) and turbid (■) water conditions. (a) Prey consumed by pike alone and in the presence of black bullhead and (b) prey consumed by black bullhead alone and in the presence of pike. **, $P < 0{\cdot}01$; NS, $P > 0{\cdot}05$.

on roach (Boët, 1980), black bullhead predation was mainly directed towards dead or injured fish lying on the bottom. It can therefore be considered that direct predation of black bullhead hardly affected roach abundance, and consequently that black bullhead do not directly compete with pike. This result is probably influenced by roach size and although using smaller roach would probably increase the predatory success of black bullhead, such a fish combination would not have been realistic in regard to the size structure of wild roach populations during the period selected to run the experiments (autumn). It also seems unlikely that the reduction in pike predation efficiency was related to interactions between roach and black bullhead. Indeed, prey movement generally increases in the presence of multiple predator species (Eklöv & VanKooten, 2001) leading to an increase in predator–prey encounter rates, which therefore 'pushes' prey to adopt riskier behaviour (Soluk & Collins, 1988; Wissinger & Mc Grady, 1993). If this were the case, black bullhead would have increased the number of roach encounters with pike, and hence led to an increase in pike predation efficiency.

Finally, the hypothesis of behavioural interference between pike and black bullhead is the most likely explanation of the reduction of pike predatory efficiency. According to Sih *et al.* (1985), predatory species may interfere with each other, thus decreasing their combined effects on prey populations. In this study, a non-additive predation effect of pike and black bullhead on roach was detected, corresponding to a reduction of the predation risk for roach. Indeed, pike predation tactics consists in a complex succession of behavioural components after prey selection, which consists in a slow approach of the prey preceding attack, capture and ingestion (Harper & Blake, 1990). Interference during this succession of behavioural phases in pike feeding strongly reduces its foraging success (Nilsson *et al.*, 2006). Because 1+ year black bullhead (1) have an activity peak during the day (Darnell & Meierotto, 1965) that corresponds to the feeding period of pike (Bruslé & Quignard, 2001) and (2) are known to exhibit aggressive behaviour against all the species they encounter (Karp & Tyus, 1990); the repeated nips of black bullhead against pike (black bullhead nips against pike were observed several times each day) probably disturbed the foraging behaviour of the pike and led to a decrease in their combined success through pike predation. Black bullhead nips against pike were frequently observed in this study, but were not quantified as they were only observable in CW experiments (in TW experiments, water was not sufficiently clear to enable continuous behavioural observations). No other disturbing behaviour by black bullhead towards pike that may affect the results was observed.

This study is the first to demonstrate a negative effect of the invasive black bullhead on the predatory efficiency of pike through direct interspecies interaction that probably occurs in the form of behavioural interference. Reducing predatory efficiency may affect pike growth rate and survival as well as modify prey selection (Eklöv & Hamrin, 1989). The results therefore confirm the potential negative impact of black bullhead on European native fauna, and particularly on pike which is a top predator considered as vulnerable in some European regions (Povž, 1996; Keith & Allardi, 2001). The strength of biotic interactions, however, is known to be influenced by environmental characteristics such as fish density, structure of the environment or resource availability (Eklöv & VanKooten, 2001; Blanchet *et al.*, 2006). Although laboratory experiments cannot reproduce the complexity of the natural environment, the experiments were designed to fit the environmental conditions found in most European reservoirs and lakes. The autumn period was selected as it corresponds to a low-water period in most south European reservoirs and lakes due to water withdrawal for agriculture and power generation (Brosse, 2000; Brosse *et al.*, 2007). Hence, fish density increases a lot due to the drastic reduction of the water volume, increasing encounter rates between fishes. This is particularly true for black bullhead that occurs in high biomass and densities in most European lowland lakes (Boët, 1980; Cucherousset *et al.*, 2006; Louette & Declerck, 2006). Moreover, the water level decrease leads to the disappearance of aquatic vegetation, and hence strongly reduces habitat complexity. This means that the spatial fish assemblage patterns found during summer no longer exist (Brosse, 2000; Brosse *et al.*, 2007) and all fishes share the same habitat. Such a homogeneous environment, as well as the high fish density, is consistent with the laboratory design. Finally, the sizes for the fishes in this study are those found during autumn in the natural environment. Nevertheless, the results based on laboratory experiments need to be tested in natural environments to allow generalization. In addition, behavioural observations would provide interesting insights into the interactions between pike and black bullhead. Combining field and laboratory results would enable management priorities to be established based on the best scientific assessment of the impact of black bullhead on pike predatory efficiency, prey selection, growth and survival and hence on the structure of native fish assemblages.

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