Journal for Nature Conservation 50 (2019) 125713

Contents lists available at ScienceDirect

Journal for Nature Conservation

journal homepage: www.elsevier.com/locate/jnc

Native top-predator cannot eradicate an invasive fish from small pond ecosystems

David Beaune[a,b,*], Franck Castelnau[a], Yann Sellier[a], Julien Cucherousset[c]

[a] Réserve Naturelle Nationale du Pinail, GEREPI, Moulin de Chitré, 86210 Vouneuil sur Vienne, France
[b] Biogéosciences, UMR 6282 CNRS, Université Bourgogne, Franche-Comté 6 Boulevard Gabriel, 21000 Dijon, France
[c] CNRS Laboratoire Évolution & Diversité Biologique, Université Paul Sabatier, Toulouse, France

A R T I C L E I N F O

Keywords:
Biological invasion
Esox lucius
Freshwater
Predator-prey interaction
Lepomisgibbosus
Biomanipulation
Biocontrol

A B S T R A C T

Pumpkinseed (*Lepomis gibbosus*) originates from North America and has been widely introduced in Europe where invasive populations have established. We tested the effectiveness of a biomanipulation approach based on the stocking of a native top-predatory species, the northern pike (*Esox lucius*), in 23 small and oligotrophic ponds at the Pinail Nature Reserve (Vienne, France) among which 10 ponds were stocked twice. In addition, 16 ponds with similar environmental characteristics were used as control with no pike stocking. Our study revealed that, even with limited space and limited alternative prey species, northern pike did not eradicate pumpkinseed populations. Instead, we found that pumpkinseed were younger and larger when reaching sexual maturity in the stocked ponds, suggesting an increased growth rate in ponds with the predator. These results suggest that invasion populations might adapt and respond to management practices. These changes were likely driven by an adaptation to predation pressure and/or changes in food availability with reduced intraspecific competition. Importantly, such changes might actually modify the level of invasiveness potential of non-native populations and lead to counterproductive results for managers.

1. Introduction

The introduction of non-native freshwater fish is a widespread phenomenon and invasive fish have been reported to induce important ecological impacts across different levels of biological organization (Cucherousset & Olden, 2011). A widely introduced species is pumpkinseed (*Lepomis gibbosus* (Linnaeus, 1758); Perciformes: Centrarchidae) that originated from North America and that has been introduced in many countries across the globe (Copp & Fox, 2007). Reported ecological impacts of pumpkinseed are primarily direct through the consumption of native prey and competition with native consumers (Préau et al., 2017). Indeed, pumpkinseed is omnivorous and prey mainly on invertebrates of various groups (García-Berthou & Moreno-Amich, 2000; Gkenas, Magalhães, Cucherousset, Domingos, & Ribeiro, 2016). In Western Europe, the species has been reported to display a latitudinal gradient in terms of population invasiveness whereby southern populations are considered as more prolific and more invasive than northern populations (Cucherousset et al., 2009).

In France, the species is legally classified as invasive (Guevel, 1997) and managers are legally required to control the species. The management of invasive freshwater fish is challenging (Britton, Gozlan, & Copp, 2011) and the most common measure used in the country to eradicate pumpkinseed is the removal of specimens caught by anglers, although the efficiency of such a method is limited (Evangelista, Britton, & Cucherousset, 2015). In some areas, novel approaches to control invasive fish species have been tested, including biocontrol through the introduction of native predators (hereafter referred to as *biomanipulation*), which has been reported in some cases as efficient for controlling invasive species in freshwater ecosystems (Britton et al., 2011).

In the present study, we tested the efficiency of a biocontrol approach in the Pinail Nature Reserve (Vienne, Nouvelle Aquitaine, Northwest France). This area is composed of 3000 permanent ponds among which approximately 20% contained pumpkinseed (Préau et al., 2017). While the introduction history of the species in this area remains largely unknown, the species has been observed impacting several native taxa with high conservation values such as amphibians (e.g. *Triturus marmoratus* and *Hyla arborea*), white-clawed crayfish (*Austropotamobius pallipes*) and probably other invertebrates (Castelnau, Sellier, & Beaune, 2016; Préau et al., 2017). Consequently, eradicating

* Corresponding author at: Réserve Naturelle Nationale du Pinail, GEREPI, Moulin de Chitré, 86210 Vouneuil sur Vienne, France.
E-mail addresses: david.beaune@u-bourgogne.fr (D. Beaune), franck.castelnau@gmail.com (F. Castelnau), sellieryann@gmail.com (Y. Sellier), julien.cucherousset@univ-tlse3.fr (J. Cucherousset).

https://doi.org/10.1016/j.jnc.2019.125713
Received 15 November 2018; Received in revised form 13 June 2019; Accepted 13 June 2019

the species from these ecosystems with high conservation values is crucial for local managers. Initial tests to eradicate pumpkinseed from the ponds included angling, netting and electrofishing but were, overall, inefficient (Sellier, 2013). Therefore, the efficiency of a biomanipulation approach based in the introduction of a native top predator, the Northern pike (*Esox lucius*) was tested. This top carnivore is preferentially piscivore, is known to eat pumpkinseed also at the Pinail reserve and the species foraging strategy is based on active ambush predation (Castelnau et al., 2016; Chapman, Mackay, & Wilkinson, 1989; Diana, 1979). In the present study, we quantified the efficiency of this approach for eradicating pumpkinseed in very small pond ecosystems. The very small size of the pond ecosystems could be considered as increasing the likelihood of successful eradication and should be the first step to try before aiming to develop the same approach in larger systems. We specifically tested the hypothesis that, due to the high predator stocking density and the small size of the ecosystems with limited alternative prey, predation by Northern pike should lead to the eradication of pumpkinseed three years after pike stocking. Pike were stocked twice in some ponds and we hypothesize that this additional stocking would lead to a higher rate of eradication in these ponds.

2. Materials and methods

2.1. Study area

The Nature Reserve of the Pinail (Réserve Naturelle Nationale du Pinail, 135 ha, N 46° 42' 2.698"- E 0° 31' 13.378") is a unique ecosystem that contains a high concentration of 5013permanent and temporary ponds (Fig. 1). These ponds are artificial and were created by millstone extraction starting at the Roman age. Ponds are filled by rainwater and some are interconnected while others are fully isolated. Ponds are colonised by macrophytes composed mainly of *Utricularia australis*, *U. bremii*, *Potamogeton polygonifolius*, *P. natans*, *Myriophyllum alterniflorum*, *Nymphaea alba* (see Beaune, Sellier, Lambert, & Grandjean, 2018 for details). Both freshwater and terrestrial ecosystems in the Nature Reserve have a high conservation value. Indeed, it forms a very rich ecological complex where more than 2 613 plant and animal species have been reported so far. The area is surrounded by 4166 ha of forest mainly classified with the Natura 2000 status (ZSC: special zone of preservation and ZPS: zone of special protection), ZICO (Zone of Europe community interest for birds; European Nature Protection area network) and ZNIEFF (Natural Zone of Ecological Interest Fauna and Flora).

The study area is covered with diversified *Erica* moors on acid and oligotrophic ground (podzol) resulting from human pasturing and burning (Pernat, Sellier, Préau, & Beaune, 2017). For centuries, humans have used the ponds as temporary reservoirs for fish and several native and non-native species have been introduced in these initially fishless ecosystems (Beaune, Sellier, Lambert et al., 2018), including *Ameiurus melas* (Rafinesque, 1820); *Anguilla anguilla* (Linnaeus, 1758); *Carassius auratus* (Linnaeus, 1758); *Carassius carassius* (Linnaeus, 1758); *Cyprinus carpio* Linnaeus, 1758; *Esox lucius* Linnaeus, 1758; *Lepomis gibbosus* (Linnaeus, 1758); *Leucaspius delineatus* (Heckel, 1843); *Rutilus rutilus* (Linnaeus, 1758); *Scardinius erythrophthalmus* (Linnaeus, 1758); *Tinca tinca* (Linnaeus, 1758). Unfortunately, no information is available on the history of introduction of fish, including pumpkinseed, in these ecosystems.

2.2. Biomanipulation and population monitoring

In 2013, a total of 39 ponds known to contain pumpkinseed in 2013 and 2005 were randomly selected. These ponds as all ponds of the Pinail are relatively small (Fig. 1), with an average area of 92.3 ± 20.3 m^2 and water depth ranging from 1 to 2.6 m with an

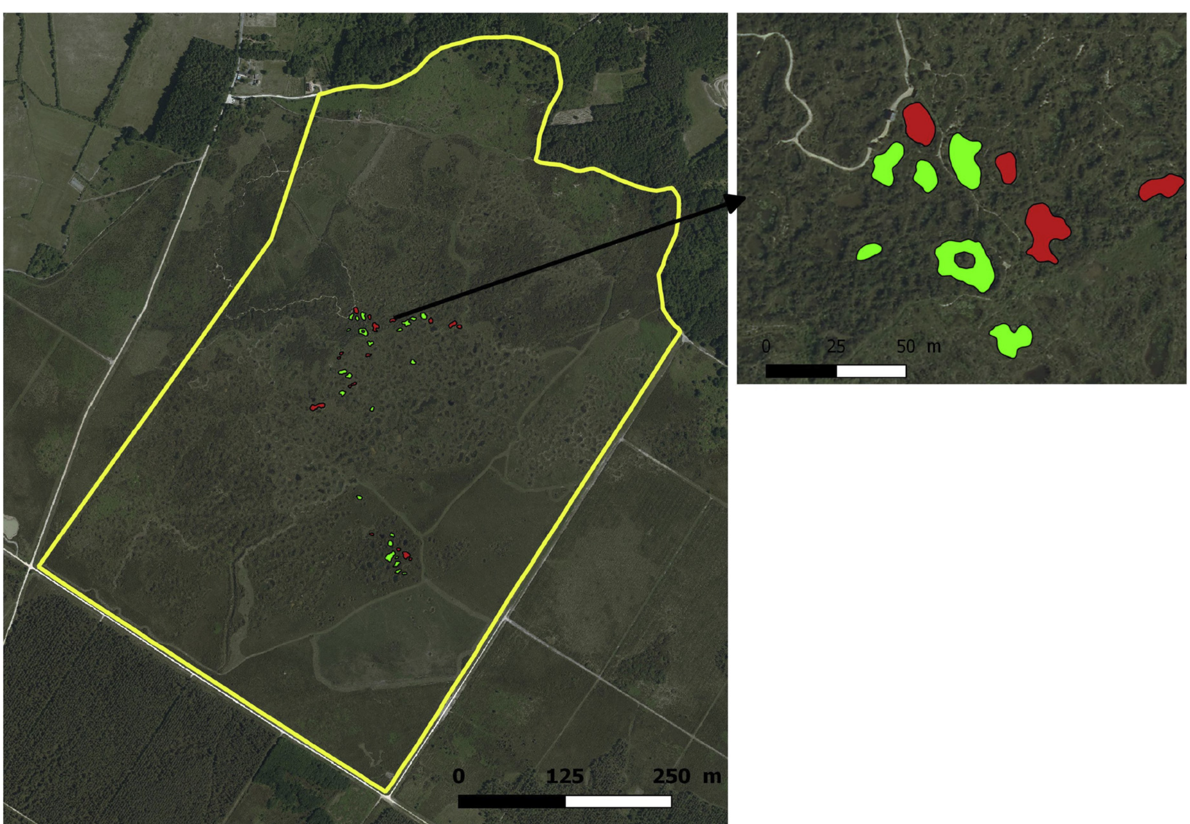

Fig. 1. Areal picture of the study area (Réserve naturelle nationale of the Pinail, France) containing more than 3000 ponds with water permanently (yellow lines). Biomanipulated pond (with pike stocking, n = 23) are displayed in green and control pond (no pike, n = 16) are displayed in red.

average of 1.6 m. The physicochemical parameters of these ponds were similar to the majority of the acidic ponds of the Pinail (pH < 6.8) with similar vegetation covers (Beaune, Sellier, Lambert et al., 2018; Beaune, Sellier, Luquet, & Grandjean, 2018). In addition, the diversity in alternative prey for pike is very limited: with *L. gibbosus* presence, there is no crayfish, few amphibians (Préau et al., 2017) and in the ponds of the study no other fish were captured (Castelnau et al., 2016). Because there was a low level of variability in physicochemical parameters between ponds (Beaune, Sellier, Luquet et al., 2018; Castelnau et al., 2016), we assume that all pumpkinseed populations were experiencing similar environmental conditions before pike introduction and had similar life-history traits (age and size distribution, age at sexual maturity). This assumption was reinforced by a random allocation of the ponds to each treatment: 16 ponds were used as control (no pike stocking and pike absent) and 23 ponds were used as treatment (pike stocked). A total of 649 young-of-the-year (YOY) pike (TL approximately 5 cm) able to feed on *L. gibbosus* were introduced in the stocked ponds with an average density of 32 individuals per pond (averaging 7 YOY/m^2) in 2013. Because pumpkinseed were still visually recorded in some treated ponds after a year (2014), a second introduction of additional pike was decided for 10 out of the 23 ponds initially stocked with pike. A total of 374 YOY pike measuring approximately 5 cm TL were introduced in the same proportion (35–40) into the 10 ponds in 2014.

Three years after the initial pike introduction (i.e. April and May 2016), the presence of pike in the stocked pond was quantified using angling. Here, angling with lure was used because ecosystems were small and to minimize the potential negative effects of sampling of other biological taxa such as amphibians as sampling was performed during their reproduction period. The aim here was to assess whether pike were still present (occurrence) and not to assess density, therefore the angling protocol was based on a first trial (15 min). If no pike were detected, the first trial was followed by a maximum of three additional trials performed every two days. If no pike were detected in these small pond systems after four trials, the pike population was assumed to be extirpated from such small system. Although this could lead to false-negative, the underestimation of pike occurrence would not impact our results qualitatively. The presence of *L. gibbosus* was also first assessed using angling (hooks baited with maggots) in both control and stocked ponds. We started with an initial 30 min trial. If no individual was caught, two additional trials were performed with two-day intervals. If no individual was caught by angling, two sessions using baited minnow traps (five traps per pond) were performed. Captured pumpkinseed were measured for body length ($\pm$ 1 mm) and mass ($\pm$ 0.1 g) and scales sample taken for age determination (Fig. 2).

2.3. Statistical analyses

The proportion of ponds containing pumpkinseed was compared between the treatments (one stocking event and two stocking events) and control ponds using a Chi Square test. Based on individuals captured using the same technique (i.e. angling, n = 40), difference in the body length and age of pumpkinseed was compared between control and treated ponds (one stocking event and two stocking events) using non-parametric Wilcoxon rank sum test. All statistical analyses were performed using R 2.11R (R Core Team, 2011). The software FiSAT II was used to perform non-linear estimation of growth parameters (the curvature parameter of the von Bertalanffy Growth Function (K) and the asymptotic length ($L\infty$) from length-at-age data (i.e. total length ($\pm$ 1 mm) and age (years) determined from scales reading; no pumpkinseeds larger than 70 mm TL were captured); see Gayanilo, Sparre, & Pauly, 2005. The parameters of the Von Bertalanffy growth formula (VBGF) are estimated from: $= L\infty(1 - \exp^{(-K(t-t0))})$; Lt being the lenght reached by a fish at age t. The growth performance index (Φ') was quantified using (Pauly & Munro, 1984) formula: $\Phi' = \log_{10}K + 2\log_{10}L\infty$. The natural mortality (M) was estimated from the Rikhter and Efanov's method (Rikhter & Efanov, 1976). With the function $M = ((1.52/t_{mass})\cdot0.72) - 0.16$; where t_{mass} is the age at first maturity (the fish of the two treatments were pooled as no biological trait history differed).

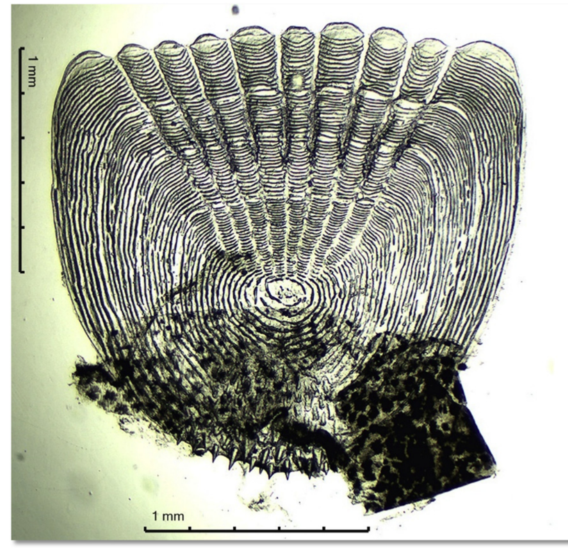

Fig. 2. Scale of a mature female of *Lepomis gibbosus* (Age 4) with four visible annuli in the Pinail nature reserve, France.

2.4. Ethical statement

Introduced fish (pike) and invasive pumpkinseed were not reintroduced in the habitat after they were captured, but were immediately euthanized by cranial percussion. Ethical approval was received from the scientific board of the National Reserve in compliance with the national guideline.

3. Results

In total, we found that pike growth in all ponds after a year and were still present three years later in at least 63.6% of the stocked ponds since pike were captured or observed in 14 of the 23 stocked ponds (7/13 in ponds with one stocking event and 7/10 in ponds with two stocking events). The minimum size of the captured pike was 30 cm, maximum size 60 cm (mean: 43.6 cm $\pm$ SE 3.26 cm, CI_{95} [36.2 cm–50.9 cm]). The largest individual weighed 1283 g and the thinnest 188 g (mean: 539.2 g $\pm$ 135.2 g, CI_{95} [233.3 g–845.1 g]).

There was a significantly higher occurrence of pumpkinseed in ponds where pike were stocked twice than in control ponds ($\chi^2 = 4.875$, df = 1, p = 0.027) while there was no significant difference between ponds where pike were stocked once and control ponds ($\chi^2 = 1.7561$, df = 1, p = 0.185). Indeed, pumpkinseed (n = 56) was sampled in 10/10 stocked ponds with two stocking events,11/13 with one stocking event and in 10/16 of the control ponds (Fig. 3).

Pumpkinseed were significantly younger in stocked ponds (average age = 2.1 y $\pm$ SE 0.2 and 3.4 y $\pm$ 0.1 in treatment and control ponds, respectively; Wilcoxon rank sum test, W = 231.5, $p < 0.001$) and had a significantly larger body size (average length =76 mm $\pm$ 3 and 67 mm $\pm$ 4 in treatment and control ponds, respectively; W = 103, p = 0.014) than in control ponds, suggesting that pumpkinseed grew faster in stocked ponds. Females from stocked ponds were mature (with gonads) at Age 2 while females from control ponds were mature at Age 3. This was confirmed by the von Bertalanffy growth rate $K = 1.49/\text{year}^{-1}$in stocked ponds (N = 16) and $0.54/\text{year}^{-1}$in control ponds (N = 24). $L\infty$ averaged 7.9 cm in stocked ponds and 8.31 cmin control ponds. Φ' was 1.244in stocked ponds and 0.384 in control ponds. The

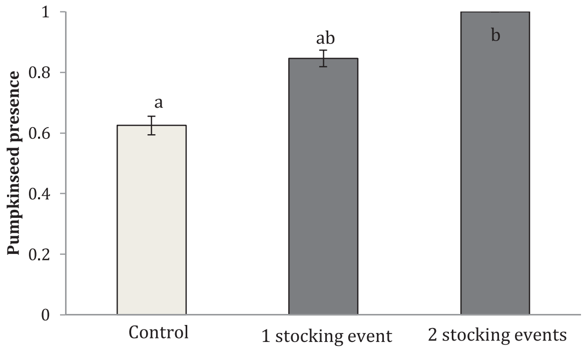

Fig. 3. Occurrence of pumpkinseed (*Lepomis gibbosus*) (mean ± SD) in the control ponds (left bar, n = 16), the treated ponds with one pike (*Esox lucius*) stocking (n = 13) and the treated ponds with two pike stockings (right bar, n = 10). Different letters indicate significant difference between treatments.

Table 1
Occurrence of pumpkinseed (*Lepomis gibbosus*) and biological parameters of pumpkinseed three years after pike (*Esox lucius*) stocking in stocked (n = 23) and control (n = 16) ponds.

Variables	Control ponds	Stocked ponds
Pumpkinseed occurrence (%)	63	91
Growth Function (K, year^{-1})	0.54	1.49
Asymptotic length (L_∞, in cm)	8.3	7.9
Growth performance index (Φ')	0.384	1.244
Natural mortality (M, year^{-1})	0.529	0.763

natural mortality coefficient of fish from the stocked ponds was M = 0.763 while it was 0.529 in the control ponds (Table 1).

4. Discussion

The present study demonstrated the complexity of managing an invasive fish species following its successful establishment in the wild. In small pond ecosystems with high conservation value, biomanipulation with native predatory fish appeared to managers as one of the most appropriate approaches since other methods such as trapping, poisoning or draining would induce important ethical and conservation issues. Although pike are active predators of pumpkinseed (confirmed by stomach content analyses in the study area, Castelnau et al., 2016) and the studied ecosystems are small with very limited alternative prey, predator stocking did not result in full eradication of invasive pumpkinseed populations. Furthermore, we found that the response to pike stocking of invasive populations might lead to counterproductive effects by reducing the negative density-dependent effects caused by competition for resources, and by decreasing the pumpkinseed age at maturity. Although it should be interpreted carefully, based on life-history traits (age at maturity and juvenile growth rate (Cucherousset et al. (2009), pumpkinseed from the stocked ponds could be categorized as 'invasive' while it is not the case for populations from the control ponds.

The pike has already been used to control invasive populations such as topmouth gudgeon (*Pseudorasbora parva*) (Lemmens, Mergeay, Vanhove, De Meester, & Declerck, 2015), American bullfrogs (*Lithobates catesbeianus*) (Louette, 2012) and red-swamp crayfish (*Procambarus clarkii*) (Neveu, 2001) with variable success. In the present study, pike stocking even in very high density (higher than the models of Skov & Nilsson, 2007), was not efficient to eradicate pumpkinseed population over a three-year period. Although it is difficult to predict and it remains to be tested, we hypothesize that a longer duration of pike presence would be unlikely to eradicate pumpkinseed in these pond ecosystems. Pike are known as being very efficient predator in freshwater ecosystems. However, the environmental conditions of the studied ponds might limit their efficiency to capture pumpkinseed. Indeed, the studied pond had a high level of macrophytes. These macrophytes, needed for pike establishment, are also plausible refuges for prey fish that might prevent their complete eradication by pike (Diehl, 1988; Heck & Crowder, 2012).

Fish life history traits have been widely reported to change with predator selective pressure and changes in resource availability (Arendt & Wilson, 1997; Ball & Baker, 1996; Coleman & Wilson, 1998; Popiel, Pérez-Fuentetaja, McQueen, & Collins, 1996; Robinson & Wilson, 1996; Wilson, Coleman, Clark, & Biederman, 1993) and pumpkinseed can also respond to management pressure (Evangelista et al., 2015). Here, we found that pumpkinseed populations in biomanipulated ponds were younger, sexually mature earlier and larger, with a faster growth rate. Although density data could not be gathered here, biomanipulation might have modified population density, releasing intraspecific competition and increasing food availability. Therefore, this might modify the dynamic of invasive populations and their potential ecological impacts. Pike may have disappeared from some ponds due to insufficient resource availability even in ponds where pumpkinseed are still present. However, the stomach content analyses revealed that pike also consumed invertebrates (Castelnau et al., 2016). The absence of capture of pumpkinseed in some control ponds may have been caused by local extirpation of populations due to an overexploitation of trophic resources and/or populations occurring at very low fish density.

In conclusion, the present study highlights that, in small pond ecosystems with limited alternative prey availability, the introduction of native top predator was not sufficient to fully eradicate invasive pumpkinseed. In addition, we found that biomanipulation induced changes in the life history traits of the invader that were likely driven by an adaptation to predation pressure and/or changes in food availability with reduced intraspecific competition. Such changes are likely to modify the ecological impacts of invasive species on native organisms (e.g. invertebrates, amphibians) and recipient ecosystems (Závorka et al., 2018), but this remains to be quantified.

Acknowledgments

We are grateful to the DREAL (Directions Régionales de l'Environnement, de l'Aménagement et du Logement) Aquitaine - Limousin - Poitou-Charentes, the SyRVA and the Agence de l'Eau Loire-Bretagne for financial contributions. JC was supported by the ERADINVA project (Convention ONEMA UPS 2017/019).

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