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

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18 **Abstract**

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

34

35 **Keywords** biological invasion • *Esox lucius* • freshwater • predator-prey interaction •
36 *Lepomisgibbosus* • biomanipulation • biocontrol

37

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43 **Introduction**

44 The introduction of non-native freshwater fish is a widespread phenomenon and invasive fish
45 have been reported to induce important ecological impacts across different levels of biological
46 organization(Cucherousset and Olden, 2011). A widely introduced species is pumpkinseed
47 (*Lepomis gibbosus* (Linnaeus, 1758); Perciformes: Centrarchidae) that originated from North
48 America and that has been introduced in many countries across the globe(Copp and Fox,
49 2007). Reported ecological impacts of pumpkinseed are primarily direct through the
50 consumption of native prey and competition with native consumers(Préau et al., 2017).
51 Indeed, pumpkinseed is omnivorous and prey mainly on invertebrates of various groups
52 (García-Garcia-Berthou and Moreno-Amich, 2000, Gkenas et al., 2016). In Western Europe,
53 the species has been reported to display a latitudinal gradient in term of population
54 invasiveness whereby southern populations are considered as more prolific and more invasive
55 than northern populations (Cucherousset et al., 2009).

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

65 In the present study, we tested the efficiency of a biocontrol approach in the Pinail
66 Nature Reserve (Vienne, Nouvelle Aquitaine, Northwest France).This area is composed of
67 3000 permanent ponds among which approximately 20 % contained pumpkinseed(Préau et

68 al., 2017). While the introduction history of the species in this area remains largely unknown,
69 the species has been observed impacting several native taxa with high conservation values
70 such as amphibians (e.g. *Triturus marmoratus* and *Hyla arborea*), white-clawed crayfish
71 (*Austropotamobius pallipes*) and probably other invertebrates (Castelnaud et al., 2016, Préau et
72 al., 2017). Consequently, eradicating the species from these ecosystems with high
73 conservation values is crucial for local managers. Initial tests to eradicate pumpkinseed from
74 the ponds included angling, netting and electrofishing but were, overall, inefficient (Sellier,
75 2013). Therefore, the efficiency of a biomanipulation approach based in the introduction of a
76 native top predator, the Northern pike (*Esox lucius*) was tested. This top carnivore is
77 preferentially piscivore, is known to eat pumpkinseed also at the Pinail reserve and the
78 species foraging strategy is based on active ambush predation (Diana, 1979, Chapman et al.,
79 1989, Castelnaud et al., 2016). In the present study, we quantified the efficiency of this
80 approach at eradicating pumpkinseed in very small pond ecosystems. The very small size of
81 the pond ecosystems could be considered as increasing the likelihood of successful
82 eradication and should be the first step to try before aiming at developing the same approach
83 in larger systems. We specifically tested the hypothesis that, due to the high predator stocking
84 density and the small size of the ecosystems with limited alternative prey, predation by
85 Northern pike should lead to the eradication of pumpkinseed three years after pike stocking.
86 Pike were stocked twice in some ponds and we hypothesize that this additional stocking
87 would lead to a higher rate of eradication in ponds stocked twice.

88

89 **Materials and methods**

90 *Study area*

91 The Nature Reserve of the Pinail (Réserve Naturelle Nationale du Pinail, 135 ha, N 46° 42'
92 2.698"- E 0° 31' 13.378") is a unique ecosystem that contains a high concentration of

93 5013 permanent and temporary ponds (Figure 1). These ponds are artificial and were created
94 by millstone extraction starting at the Roman age. Ponds are filled by rainwater and some are
95 interconnected while others are fully isolated. Ponds are colonised by macrophytes composed
96 mainly of *Utricularia australis*, *U. bremii*, *Potamogeton polygonifolius*, *P. natans*,
97 *Myriophyllum alterniflorum*, *Nymphaea alba* (see Beaune et al., 2018a for details). Both
98 freshwater and terrestrial ecosystems in the Nature Reserve have a high conservation value.
99 Indeed, it forms a very rich ecological complex where more than 2 613 plant and animal
100 species have been reported so far. The area is surrounded by 4166 ha of forest mainly
101 classified with the Natura 2000 status (ZSC: special zone of preservation and ZPS: zone of
102 special protection), ZICO (Zone of Europe community interest for birds; European Nature
103 Protection area network) and ZNIEFF (Natural Zone of Ecological Interest Fauna and Flora).

104 The study area is covered with diversified *Erica* moors on acid and oligotrophic
105 ground (podzol) resulting from human pasturing and burning (Pernat et al., 2017). For
106 centuries, humans have used the ponds as temporary reservoirs for fish and several native and
107 non-native species have been introduced in these initially fishless ecosystems (Beaune et al.,
108 2018a), including *Ameiurus melas* (Rafinesque, 1820); *Anguilla anguilla* (Linnaeus, 1758);
109 *Carassius auratus* (Linnaeus, 1758); *Carassius carassius* (Linnaeus, 1758); *Cyprinus carpio*
110 Linnaeus, 1758; *Esox lucius* Linnaeus, 1758; *Lepomis gibbosus* (Linnaeus, 1758); *Leucaspius*
111 *delineatus* (Heckel, 1843); *Rutilus rutilus* (Linnaeus, 1758); *Scardinius erythrophthalmus*
112 (Linnaeus, 1758); *Tinca tinca* (Linnaeus, 1758). Unfortunately, no information is available on
113 the history of introduction of fish, including pumpkinseed, in these ecosystems.

114

115 ***Bio-manipulation and population monitoring***

116 In 2013, a total of 39 ponds known to contain pumpkinseed in 2013 and 2005 were randomly
117 selected. These ponds as all ponds of the Pinail are relatively small (Figure 1), with an

118 average area of $92.3 \pm 20.3 \text{ m}^2$ and water depth ranging from 1 to 2.6 m with an average of
119 1.6 m. The physicochemical parameters of these ponds were similar to the majority of the
120 acidic ponds of the Pinail ($\text{pH} < 6.8$) with similar vegetation covers (Beaune et al., 2018a,
121 Beaune et al., 2018b). In addition, the diversity in alternative prey for pike is very limited:
122 with *L. gibbosus* presence, there is no crayfish, few amphibians (Préau et al., 2017) and in the
123 ponds of the study no other fish were captured (Castelnaud et al., 2016). Because there was a
124 low level of variability in physicochemical parameters between ponds (Castelnaud et al., 2016;
125 Beaune et al. 2018b), we assume that all pumpkinseed populations were experiencing similar
126 environmental conditions before pike introduction and had similar life-history traits (age and
127 size distribution, age at sexual maturity). This assumption was reinforced by a random
128 allocation of the ponds to each treatment: 16 ponds were used as control (no pike stocking and
129 pike absent) and 23 ponds were used as treatment (pike stocked). A total of 649 young-of-the-
130 year (YOY) pike (TL approximately 5 cm) able to feed on *L. gibbosus* were introduced in the
131 stocked ponds with an average density of 32 individuals per pond (averaging 7 YOY/m²) in
132 2013. Because pumpkinseed were still visually recorded in some treated ponds after a year
133 (2014), a second introduction of additional pike was decided for 10 out of the 23 ponds
134 initially stocked with pike. A total of 374 YOY pike measuring approximately 5 cm TL were
135 introduced in the same proportion (35-40) into the 10 ponds in 2014.

136 Three years after the initial pike introduction (i.e. April and May 2016), the presence
137 of pike in the stocked pond was quantified using angling. Here, angling with lure was used
138 because ecosystems were small and to minimize the potential negative effects of sampling of
139 other biological taxa such as amphibians as sampling was performed during their reproduction
140 period. The aim here was to assess whether pike were still present (occurrence) and not to
141 assess density, therefore the angling protocol was based on a first trial (15 min). If no pike
142 were detected, the first trial was followed by a maximum of 3 additional trials performed

143 every 2 days. If no pike were detected in these small pond systems after 4 trials, the pike
144 population was assumed to be extirpated from such small system. Although this could lead to
145 false-negative, the underestimation of pike occurrence would not impact our results
146 qualitatively. The presence of *L. gibbosus* was also first assessed using angling (hooks baited
147 with maggots) in both control and stocked ponds. We started with a first 30 min trial. If no
148 individual was caught, two additional trials were performed with two-day intervals. If no
149 individual was caught by angling, two sessions using baited minnow traps (5 traps per pond)
150 were performed. Captured pumpkinseed were measured for body length (± 1 mm) and mass
151 (± 0.1 g) and scales sample taken for age determination (Figure 2).

152

153 ***Statistical analyses***

154 The proportion of ponds containing pumpkinseed was compared between the treatments (one
155 stocking event & two stocking events) and control ponds using a Chi Square test. Based on
156 individuals captured using the same technique (i.e. angling, $n = 40$), difference in the body
157 length and age of pumpkinseed was compared between control and treated ponds (one
158 stocking event & two stocking events) using non-parametric Wilcoxon rank sum test. All
159 statistical analyses were performed using R 2.11R (R Development Core Team, 2011). The
160 software FiSAT II was used to perform non-linear estimation of growth parameters (the
161 curvature parameter of the von Bertalanffy Growth Function (K) and the asymptotic length
162 (L_{∞}) from length-at-age data (i.e. total length (± 1 mm) and age (years) determined from
163 scales reading; no pumpkinseeds larger than 70 mm TL were captured). See Gayanilo et al.,
164 2005. The parameters of the Von Bertalanffy growth formula (VBGF) are estimated
165 from: $L_t = L_{\infty}(1 - \exp^{-K(t-t_0)})$; L_t being the length would reach a fish ate age t . The
166 growth performance index (Φ') was quantified using (Pauly and Munro, 1984) formula: $\Phi' =$
167 $\log_{10} K + 2 \log_{10} L_{\infty}$. The natural mortality (M) was estimated from the Rikhter and

168 Efanov's method (Rikhter and Efanov, 1976). With the function $M = ((1.52/t_{\text{mass}}) \cdot 0.72) - 0.16$;
169 where t_{mass} is the age at first maturity (the fish of the two treatments were pooled as no
170 biological trait history differed).

171

172 ***Ethical statement***

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

177

178 **Results**

179 In total, we found that pike growth in all ponds after a year and were still present 3 years later
180 in at least 63.6 % of the stocked ponds since pike were captured or observed in 14 of the 23
181 stocked ponds (7/13 in ponds with one stocking event and 7/10 in ponds with two stocking
182 events). The minimum size of the captured pike was 30 cm, maximum size 60 cm (mean: 43.6
183 cm \pm SE 3.26 cm, CI₉₅ [36.2 cm - 50.9 cm]). The largest individual weighed 1283 g and the
184 thinnest 188 g (mean: 539.2 g \pm 135.2 g, CI₉₅ [233.3 g - 845.1 g]).

185 There was a significantly higher occurrence of pumpkinseed in ponds where pike
186 were stocked twice than in control ponds ($\chi^2 = 4.875$, df = 1, p = 0.027) while there was no
187 significant difference between ponds where pike were stocked once and control ponds ($\chi^2 =$
188 1.7561, df = 1, p = 0.185). Indeed, pumpkinseed (n=56) was sampled in 10/10 stocked ponds
189 with two stocking events, 11/13 with one stocking events and in 10/16 of the control ponds.

190 Pumpkinseed were significantly younger in stocked ponds (average age = 2.1 y \pm SE
191 0.2 and 3.4 y \pm 0.1 in treatment and control ponds, respectively; Wilcoxon rank sum test, W =
192 231.5, p < 0.001) and had a significantly larger body size (average length = 76 mm \pm 3 and 67

193 mm \pm 4 in treatment and control ponds, respectively; $W = 103$, $p = 0.014$) than in control
194 ponds, suggesting that pumpkinseed grew faster in stocked ponds. Females from stocked
195 ponds were mature (with gonads) at Age 2 while females from control ponds were mature at
196 Age 3. This was confirmed by the von Bertalanffy growth rate $K = 1.49/\text{year}^{-1}$ in stocked ponds
197 ($N = 16$) and $0.54/\text{year}^{-1}$ in control ponds ($N = 24$). L_{∞} averaged 7.9 cm in stocked ponds and
198 8.31 cm in control ponds. Φ' was 1.244 in stocked ponds and 0.384 in control ponds. The
199 natural mortality coefficient of fish from the stocked ponds was $M = 0.763$ while it was 0.529
200 in the control ponds (Table 1).

201

202

203 **Discussion**

204 The present study demonstrated the complexity of managing an invasive fish species
205 following its successful establishment in the wild. In small pond ecosystems with high
206 conservation value, biomanipulation with native predatory fish appeared to managers as one
207 of the most appropriate approach since other methods such as trapping, poisoning or draining
208 would induce important ethical and conservation issues. Although pike are active predators of
209 pumpkinseed (confirmed by stomach content analyses in the study area, Castelnaud et al.,
210 2016) and the studied ecosystems are small with very limited alternative prey, predator
211 stocking did not allow to fully eradicate invasive pumpkinseed populations. Furthermore, we
212 found that the response to pike stocking of invasive populations might lead to
213 counterproductive effects by reducing the negative density-dependent effects caused by
214 competition for resources, and by decreasing the pumpkinseed age at maturity. Although it
215 should be interpreted carefully, based on life-history traits (age at maturity and juvenile
216 growth rate; Cucherousset et al. (2009), pumpkinseed from the stocked ponds could be
217 categorized as 'invasive' while it is not the case for populations from the control ponds.

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

231 Fish life history traits have been widely reported to change with predator selective
232 pressure and changes in resource availability (Ball and Baker, 1996, Robinson and Wilson,
233 1996, Wilson et al., 1993, Coleman and Wilson, 1998, Popiel et al., 1996, Arendt and Wilson,
234 1997) and pumpkinseed can also respond to management pressure (Evangelista et al., 2015).
235 Here, we found that pumpkinseed populations in biomanipulated ponds were younger,
236 sexually mature earlier and larger, with a faster growth rate. Although density data could not
237 be gathered here, biomanipulation might have modified population density, releasing
238 intraspecific competition and increasing food availability. Therefore, this might modify the
239 dynamic of invasive populations and their potential ecological impacts. Pike may have
240 disappeared from some ponds due to insufficient resource availability even in ponds where
241 pumpkinseed are still present. However, the stomach content analyses revealed that pike also
242 consumed invertebrates (Castelnau et al., 2016). The absence of capture of pumpkinseed in

243 some control ponds may have been caused by local extirpation of populations due to an
244 overexploitation of trophic resources and/or populations occurring at very low fish density.

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

253

254

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341

342 Figures

343

344 **Figure 1** Areal picture of the study area (Réserve naturelle nationale of the Pinail, France) containing more than
345 3000 ponds with water permanently (yellow lines). Biomanipulated pond (with pike stocking, n = 23) are
346 displayed in green and control pond (no pike, n = 16) are displayed in red.

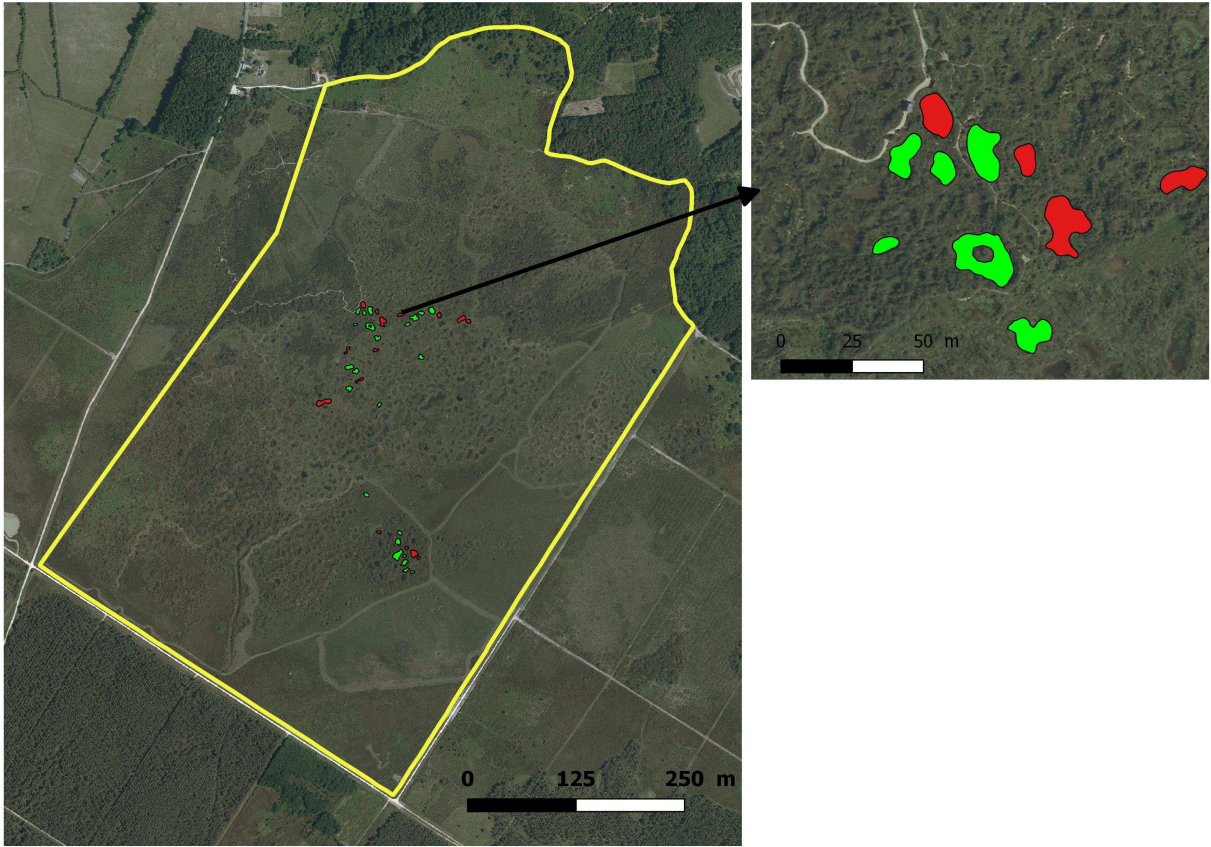
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348 **Figure 2** Scale of a mature female of *Lepomis gibbosus* (Age 4) with four visible annuli in the Pinail nature
349 reserve, France.

350

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

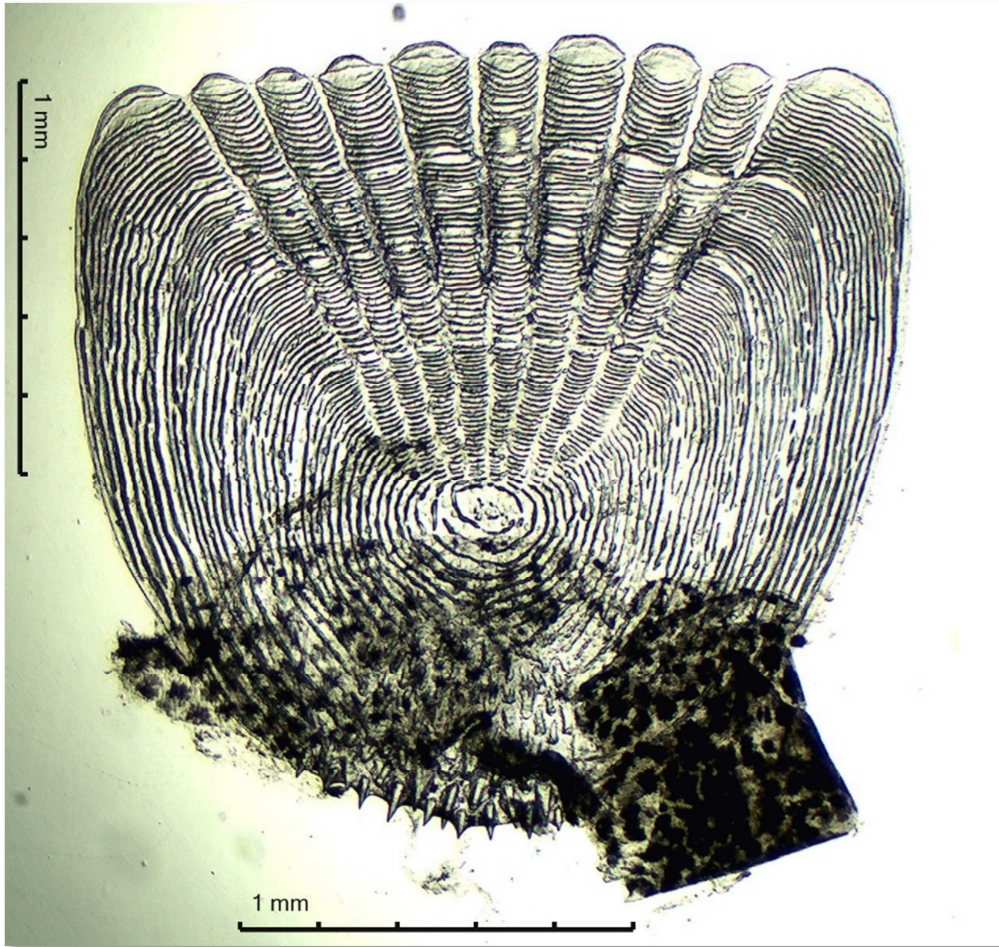
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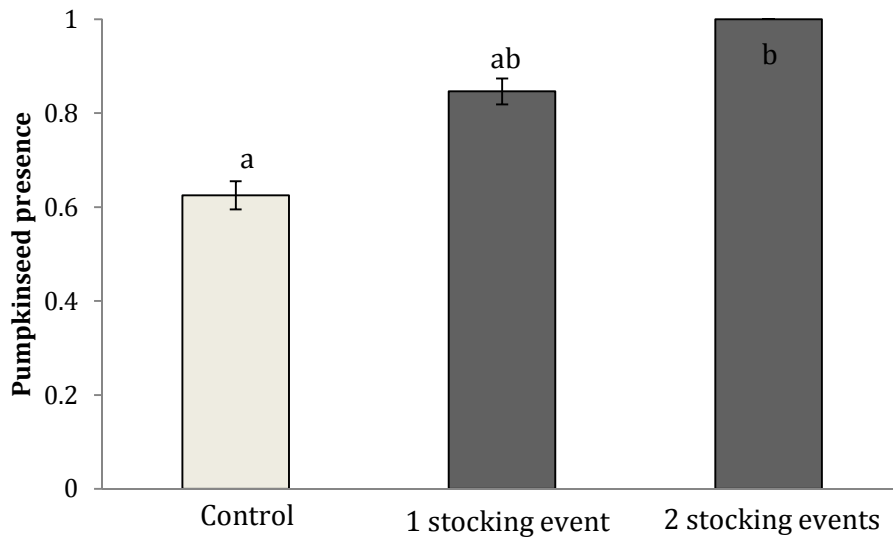
356 **Figure 1**

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359 **Figure 2**



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361 **Figure 3**

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

364

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

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