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1 **Can underwater refuges protect fish populations against cormorant**  
2 **predation? Evidence from a large scale multiple pond experiment**

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4

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11

12 **ABSTRACT**

13 Artificial structures can protect fish against predation by cormorants. However, their  
14 effectiveness in larger water bodies with different fish communities in the presence of  
15 natural vegetation still needs to be explored. Using a large scale field experiment with  
16 twenty-four ponds stocked with differently composed fish communities, the present study  
17 investigates the extent to which the effect of artificial refuges on fish is species-specific and  
18 determined by the characteristics of the fish community. This study provides strong  
19 experimental evidence for artificial refuges protecting fish against predation by cormorants,  
20 even in the presence of submerged vegetation. The effect of the refuges was, however,  
21 highly species-specific and depended on the composition of the fish community. Strong  
22 positive effects of refuges on rudd and roach populations were observed, especially in ponds  
23 where these species dominated from the start of the experiment. Overall, the total biomass  
24 of young-of-the-year, one-year-old and adult rudd and roach was on average 500, 7 and 15  
25 times lower in ponds without than in ponds with refuges, respectively. No effect of artificial  
26 refuges on other fish species were found. This study indicates that artificial refuges can  
27 facilitate the coexistence of predation vulnerable fish populations with cormorants in lakes  
28 and ponds.

29 **key words:** habitat structure, fish community composition, planktivorous species,  
30 benthivorous species, submerged aquatic vegetation, bird

31

## 32 **INTRODUCTION**

33 Cormorants (*Phalacrocorax spp.*) are known as efficient, opportunistic piscivores (Casaux *et al.* 2009; Santoul *et al.* 2004) that are not limited to shallow littoral zones, but also efficiently  
34 exploit benthic and pelagic habitats in both marine and freshwater ecosystems (Grémillet *et al.* 1998; Grémillet *et al.* 1999; Nelson 2005). The remarkable recovery of cormorant  
35 populations in many parts of the world is often considered a great success in terms of nature  
36 conservation (Young *et al.* 2010). Yet, their successful comeback fuels conflicts between  
37 different stakeholder groups worldwide (Žydelis & Kontautas 2008; Carss *et al.* 2009;  
38 Marzano *et al.* 2013; Kloskowski 2011).

41 Currently, there exists a highly polarized debate on the extent to which cormorants affect  
42 fish communities. Multiple investigations show that predation by cormorants has no or only  
43 marginal effects on fish communities (Engström 2001; Dalton *et al.* 2009; Barks *et al.* 2010;  
44 Östman *et al.* 2012). Other studies suggest that cormorants affect local fish populations  
45 negatively (Winfield *et al.* 2002; Rudstam *et al.* 2004; Steffens 2010; Salmi *et al.* 2015).  
46 Cormorants have since long been held accountable for considerable economic and socio-  
47 cultural losses at aquaculture facilities and recreational fisheries (Lekuona 2002; Russell *et al.* 1996; Feltham *et al.* 1999). To what extent and under which circumstances this is most  
48 likely to occur, remains, however, largely unclear (Doucette *et al.* 2011).

50 Cormorants are not only able to reduce fish community biomass, but may also alter the  
51 species and size-class composition through selective predation. Fish species vary in

52 vulnerability to predation, as a result of differences in body size, habitat use and anti-  
53 predator behavior (Cosolo *et al.* 2010; Suter 1997). Small fish (<15 cm) are more susceptible  
54 than large fish and typically tend to dominate the diet of cormorants foraging in standing  
55 water (Emmrich & Düttmann 2011; Suter 1997; Troynikov *et al.* 2013; Diana *et al.* 2006).  
56 Especially small percids and cyprinids are known to be particularly vulnerable to predation  
57 by cormorants (Suter 1997; Salmi *et al.* 2015; Östman *et al.* 2012; Skov *et al.* 2014).

58 Physical habitat structure is known to protect prey against predation (Putman 1994; Ellner *et*  
59 *al.* 2001). For example, macrophyte vegetation has been shown to reduce the foraging  
60 efficiency of cormorants (Eisenhower & Parrish 2009) by reducing the access to fish  
61 (Grémillet & Wilson 1999). Man-made structures may also provide shelter from predation  
62 (Orpwood *et al.* 2010). During recent decades, there is a growing interest in the use of  
63 artificial refuges to reduce fish stock losses by cormorants (McKay *et al.* 2003; Russell *et al.*  
64 2008; Orpwood *et al.* 2010; Russell *et al.* 2012). So far, experiments with artificial refuges  
65 have been promising (Russell *et al.* 2008; Russell *et al.* 2003), but remained limited to  
66 relative small ponds devoid of submerged vegetation. The effectiveness of refuges in the  
67 presence of aquatic vegetation still remains to be explored. As vegetation provides natural  
68 shelter for fish during the growth season, it may render artificial refuges superfluous.  
69 Furthermore, there are several other factors that may complicate the efficacy of refuges. For  
70 example, the extent to which fish use shelter may be largely determined by the presence of  
71 piscivorous fish. Jacobsen and Perrow (1998) showed experimentally that the presence of an  
72 ambush predator, such as pike (*Esox lucius L.*), can reduce the use of macrophytes as shelter  
73 by roach (*Rutilus rutilus L.*). If such behavioral response results in an increased exposure to  
74 cormorants, we expect that the presence of pike will reduce the protective effect of refuges.  
75 Furthermore, cormorants are highly mobile predators capable of actively selecting the most

76 suitable foraging sites in a large area (Russell *et al.* 2003; Draulans 1987; Kumada *et al.* 2013;  
77 Bugajski *et al.* 2012). Predation pressure by cormorants, and the potential of refuges to  
78 protect their prey, may therefore be more pronounced in ponds with high compared to low  
79 densities of suitable prey.

80 In this study, we tested how efficiently artificial refuges can protect fish against predation by  
81 cormorants in small, shallow ponds with natural macrophyte vegetation. Furthermore, we  
82 aimed to gain insight into the factors that may determine this refuge efficiency. Our  
83 hypothesis is that the extent to which artificial refuges protect fish against predation by  
84 cormorants is species-specific and largely determined by the characteristics of the fish  
85 community itself. We postulate that refuges are more effective in protecting small fish  
86 species compared to larger species due to negative size-selective predation by cormorants.  
87 Furthermore, due to the ability of cormorants to select for sites with high prey availability,  
88 we expect refuge effects to be more pronounced in ponds with high densities of vulnerable  
89 fish species. Finally, we hypothesize that the efficiency of refuges is lower in the presence of  
90 piscivorous fish because of increased use of open water by prey fish to avoid predation by  
91 predatory fish. To test these hypotheses, we conducted a large scale, well-replicated whole-  
92 pond experiment in which we manipulated the fish community composition of 24 shallow  
93 ponds by drainage and subsequent restocking with four differently composed fish  
94 communities; (1) small-sized planktivorous species only, (2) larger sized benthivorous species  
95 only, (3) a combination of small-sized planktivorous and larger sized benthivorous fish , and  
96 (4) a combination of both in the presence of piscivorous fish. Half of the ponds of each fish  
97 stock treatment were provided with artificial refuges.

## 98 **METHODS**

### 99 **Study area**

100 The pond experiment was performed in the region "Vijvergebied Midden-Limburg", situated  
101 in the North-eastern part of Belgium (50° 59' 00.92" N; 5° 19' 55.85" O and surroundings),  
102 and part of "De Wijers" area. The region comprises more than 1000 shallow ponds, many of  
103 which originated from the extraction of iron ore (between 1850 and 1900) and peat (until  
104 1930). Additional ponds were created after 1950 for the purpose of fish farming. Most ponds  
105 are interconnected by a complex network of rivulets. Although a majority of ponds is  
106 nowadays protected by national and international legislations (Natura 2000 status, Birds  
107 directive [79/409/EEC] and Habitats directive [92/43/ECC]) and managed for purposes of  
108 nature conservation, fish farming is still an important local practice that creates a substantial  
109 income for multiple family enterprises. Current fish farming activities are strongly directed  
110 towards farming of common carp (*Cyprinus carpio L.*), but also involve other species, such as  
111 rudd (*Scardinius erythrophthalmus L.*), roach (*Rutilus rutilus L.*), ide (*Leuciscus idus L.*), tench  
112 (*Tinca tinca L.*) and perch (*Perca fluviatilis L.*).

113 According to annual bird counts (Devos *et al.* 2011), the number of cormorants in the region  
114 has remained relatively constant during the latest decade (250-300 individuals during winter  
115 period). Although Vijvergebied Midden-Limburg is frequented by cormorants throughout  
116 the year, cormorant numbers tend to be considerably higher during the winter period when  
117 migrant birds visit the region. Currently, there is a relatively small breeding colony in  
118 Vijvergebied Midden-Limburg (approximately 15 breeding pairs). The extent to which  
119 predation by cormorants affects fish stocks in the area is strongly debated.

## 120 **Experimental design**

121 We drained twenty-four former fish farming ponds (ranging in size from 0.239 to 2.224 ha)  
122 during autumn 2008 and removed the resident fish communities. The ponds were  
123 subsequently refilled in early spring 2009. During refilling, fine mesh stainless steel grids (2  
124 mm) were placed at the inlets to minimize the entrance of wild fish. After filling, all  
125 hydrological connections with rivulets and other ponds were closed. We stocked the ponds  
126 in early March 2009 with four differently composed fish communities, all with a total initial  
127 biomass of 100 kg ha<sup>-1</sup>. Fish treatments were defined as (1) small planktivorous fish only  
128 (adult rudd and roach, one year old ide and small perch, PL); (2) benthivorous fish only (one  
129 year old common carp, B); (3) planktivorous and benthivorous fish (50 kg ha<sup>-1</sup> of each, PL+B);  
130 and (4) planktivores, benthivores and piscivores (pike fingerlings, PL+B+PI). We refer to Table  
131 1 for more details on the stocked fish communities. Each of these fish stock treatments was  
132 replicated with six randomly selected ponds. In half of the ponds of each fish treatment (n =  
133 3), we constructed cages meant to act as refuges for fish against cormorant predation. These  
134 refuges were constructed following the design of Russell *et al.* (2008) and consisted of cubic  
135 frames, covering a surface of 144 m<sup>2</sup> (Fig. S1). The four sides of the refuges were closed with  
136 nylon nets (10 cm mesh width) to make them encompass the entire water column. To  
137 enhance the attractiveness of the refuges for fish, we covered 1/3rd of their upper part with  
138 an opaque nylon cloth and created internal structure by placing pine wood branches inside  
139 each cage. The number of refuges per pond was chosen such that they covered  
140 approximately 5% of the total pond surface (cumulative surfaces per pond ranging from 179  
141 to 1197 m<sup>2</sup>). The experiment lasted almost two years (from early spring 2009 to late autumn  
142 2010) and thus incorporated an entire winter period during which predation pressure by  
143 cormorants is expected to be most pronounced since migrant birds visit the area, submerged

144 aquatic vegetation is absent and swimming speeds of fish are lower due to low water  
145 temperature.

#### 146 **Pond characteristics**

147 We assessed major environmental pond variables during the growth season (May -  
148 September) in 2009 and 2010 to ensure that observed effects of artificial refuges cannot be  
149 attributed to coincidental differences for other pond characteristics. Daytime oxygen  
150 concentrations and pH were measured in July using standard electrodes (Hach Multimeter).  
151 We collected depth-integrated water samples with a tube sampler (length: 1.2 m; diameter  
152 75 mm) at five random locations in the pelagic zone of each pond to measure the  
153 concentration of chlorophyll *a*, suspended solids and nutrients (total nitrogen, total  
154 phosphorus). *In vivo* chlorophyll *a* concentrations were determined monthly with a handheld  
155 fluorometer (AquaFluor, Turner Designs, Sunnyvale, CA). The amount of suspended solids in  
156 the water column was determined gravimetrically twice during both summers (July and  
157 August of both years) by filtering a known volume of pond water through a GF/F filter  
158 (Whatman). We measured total nutrient concentrations from July water samples with a  
159 Technicon Auto analyzer II (Technicon, Tarrytown, New York, USA) after alkaline persulphate  
160 digestion (Koroleff 1970). Water samples for the measurement of nutrients and suspended  
161 solids were stored on ice in the dark during transportation to the laboratory and were stored  
162 at -20 °C until further analysis. We visually estimated the percentages of pond surface  
163 covered by submerged, emergent and floating vegetation in August of both years.

#### 164 **Fish community assessments**

165 We assessed the total biomass, species composition and size distribution of the fish  
166 community for each pond separately at the end of the experiment in autumn 2010. Fish



167 communities were harvested via pond drainage and the use of seine nets. The collected fish  
168 were sorted into different size fractions. Large size classes of common carp, ide, rudd and  
169 roach were sorted manually. The remaining fish were sorted by using multiple consecutive  
170 nets with decreasing mesh widths (5 cm, 2 cm, 1 cm, 0.5 cm) suspended in the water. We  
171 determined the total weight of each size fraction of each pond and took one subsample (at  
172 least 10 individuals for common carp, ide and large rudd and roach; > 30 individuals for  
173 subsamples from smaller size classes) from each fraction to determine the species identity,  
174 standard body length (SL) and body weight of individuals.

#### 175 **Data analysis**

176 We reconstructed the species and size composition of the fish communities by combining  
177 the compositional data from the subsamples with the data on the biomass of the size  
178 fractions. We reconstructed the age distribution for the stocked species in each pond by  
179 assigning length cohorts to age classes. Data for rudd and roach were pooled and are further  
180 referred to as planktivorous cyprinids (YOY cyprinids, Y1Y cyprinids and adult cyprinids).

181 We applied partial redundancy analyses (RDA) to assess the unique effects of fish stock  
182 treatments, artificial refuges and their interactions on local environmental pond variables  
183 and fish community composition. Partial RDA is a canonical ordination technique designed to  
184 explore the relationships between multiple explanatory variables and a multivariate set of  
185 response variables in the presence of covariates. As such it is the multivariate equivalent of  
186 partial linear regression. We used biomass data of the fish populations in all statistical  
187 analyses. Fish biomass data and all continuous environmental variables, except pH, were log-  
188 transformed to improve distributional properties of the data. Pond variables that were  
189 measured multiple times a year were represented by their means. Most ponds contained

190 also fish species that had not been stocked by us (see also SI1). We included all fish species  
191 in the response matrices when analyzing the effects of initial stock treatments. When testing  
192 for the effects of refuges, however, we only included the species of interest to us, i.e. the  
193 initially stocked species. Significance levels were assessed with random Monte-Carlo  
194 permutations (n=999, full model) (Borcard *et al.* 2011).

195 To further explore the effects of refuges at the species and age class level, we performed  
196 ANCOVA analyses on biomass data of each stocked species and its age classes separately. In  
197 these analyses initial fish stock treatment, presence of refuges, the interaction and the  
198 percentage cover by submerged vegetation were specified as explanatory variables.

199 Partial RDA-analyses were performed in CANOCO v4.5 (Lepš & Šmilauer 2003) and all  
200 univariate analyses were done with the software package STATISTICA v10 (StatSoft, Inc.,  
201 Tulsa, Oklahoma).

## 202 **RESULTS**

203 Partial RDA analyses revealed that the experimental treatments had no effect on the set of  
204 investigated environmental pond variables in 2009 (Table 2). In contrast, we found evidence  
205 for a refuge effect in 2010. More detailed univariate analyses on data of this year indicated a  
206 lower percentage of submerged vegetation cover in ponds without refuges compared to  
207 ponds with refuges (average coverage 7.6% and 25.6%, respectively; Kruskal-Wallis test:  
208  $H_{1,23} = 5.549$ ,  $P = 0.019$ ). Ponds without refuges tended to have a lower coverage with  
209 submerged vegetation in 2010 compared to 2009 (average coverage 7.4% and 26.0%,  
210 respectively; paired T-test:  $t = 2.17$ ,  $P = 0.055$ ), whereas the coverage with submerged  
211 vegetation remained similar among years in the presence of refuges (average coverage  
212 30.0% and 25.6% in 2009 and 2010 respectively; paired T-test:  $t = 0.512$ ,  $P = 0.619$ ) (Fig. S2).

213 We found no significant differences between treatments and years for other environmental  
214 pond variables.

215 RDA analysis revealed that the refuge treatment had a marginally significant effect on fish  
216 community composition ( $R^2 = 13.2\%$ ,  $F = 1.503$ ,  $P = 0.090$ ) (Fig. 1). However, when limited to  
217 small predation vulnerable fish species, such as rudd, roach, ide and perch, RDA revealed  
218 significant interaction effects between refuges and the fish stock treatment ( $R^2 = 16.5\%$ ,  $F =$   
219  $2.323$ ,  $P = 0.040$ ). Refuge effects tended to be more pronounced in the pure planktivorous  
220 fish treatment compared to the combined fish treatments (PL+B and PL+B+Pi) (Fig. 1).

221 Additional ANCOVA analyses (Table 3) performed on the biomass data of individual species  
222 showed positive refuge effects for adult, YOY and to a lesser extent also for Y1Y  
223 planktivorous cyprinids (Fig. 2). These effects were especially strong in ponds of the  
224 planktivorous fish treatment. In this fish stock treatment, YOY fish were almost entirely  
225 absent in ponds without refuges and YOY fish biomass in these ponds was on average 500  
226 times lower than in ponds with refuges. Similarly, the biomass of Y1Y and adult planktivores  
227 was 7 and 15 times higher in the ponds with than without refuges, respectively. There was  
228 also a tendency for effects of refuges on planktivorous cyprinids in the other fish community  
229 types, but these were less pronounced and not consistent. Despite the strong positive refuge  
230 effects on planktivorous cyprinids, the biomass of adults of these species were strongly  
231 reduced by the end of the experiment in all experimental ponds (on average 90% of the  
232 initially stocked biomass). We found no indications of refuge effects on other fish species.  
233 With the exception of a positive effect on pike, we found no evidence for any effects of  
234 submerged vegetation cover on the biomass of the investigated fish species and size classes

235 (Table 3, Fig. S3). We refer to supporting information for detailed information on the overall  
236 fish community characteristics in the ponds (SI. 1).

## 237 **DISCUSSION**

238 Our study provides experimental evidence for positive effects of artificial refuges on fish  
239 populations, even in the presence of submerged aquatic vegetation. The effect of artificial  
240 refuges was, however, highly species-specific and tended to depend on the composition of  
241 the fish community itself. More specifically, we found profound positive effects of refuges on  
242 populations of rudd and roach, but not on other fish species. Positive refuge effects were  
243 more pronounced in fish communities that were dominated by these species from the  
244 beginning of the experiment. We found no evidence for an effect of pike on the efficiency of  
245 refuges.

246 The observed species-specific refuge effects are in line with our expectations. They likely  
247 resulted from interspecific differences in vulnerability to cormorant predation, although they  
248 may to some extent also reflect differences in refuge use intensity. The positive effects of  
249 artificial refuges on rudd and roach populations in our study are also consistent with results  
250 from previous investigations (Russell *et al.* 2008). In our experiment, we observed strong  
251 positive effects of artificial refuges on both juvenile (YOY and Y1Y) and adult rudd and roach.  
252 However, the density of initially stocked adults of these species was reduced considerably in  
253 all experimental ponds during the experiment. This observation suggests that predation  
254 losses of adult rudd and roach remained high, even in the presence of artificial refuges.  
255 Artificial refuges seem to have resulted in higher reproduction success of these species. We  
256 can only speculate about the exact mechanism that underlies this result. Nevertheless, our

257 study provides clear evidence that refuges can promote the viability of rudd and roach  
258 populations in the presence of cormorants on the longer term.

259 Our results indicate that the effect of refuges also depends on the characteristics of the fish  
260 community itself. Indeed, the positive effect of refuges on rudd and roach populations in our  
261 experiment tended to be much more pronounced in fish communities that were dominated  
262 by these species from the beginning of the experiment by design. This observation suggests  
263 that predation intensity by cormorants depended on the density of favored prey.  
264 Cormorants are highly mobile predators that actively select foraging sites based on the  
265 availability of suitable prey (Kumada *et al.* 2013; Grémillet & Wilson 1999; Eisenhower &  
266 Parrish 2009). Given the high suitability of roach as prey (Dirksen *et al.* 1995; Suter 1997), we  
267 argue that ponds of the planktivorous fish treatment may have been visited more frequently  
268 by foraging cormorants due to their relatively high densities of rudd and roach.

269 In contrast to our expectations, we found no evidence for an effect of pike on the  
270 effectiveness of artificial refuges. Possibly, predation by pike was too low to induce reduced  
271 use of refuges as shelter against cormorants by prey fish. Indeed, the densities of stocked  
272 pike fingerling in our experiment were considerably lower than those typically  
273 recommended as part of biomanipulation management ( $>1000$  fingerlings  $\text{ha}^{-1}$ ) (Prejs *et al.*  
274 1994; Berg *et al.* 1997). However, we aimed to assess the effect of realistic pike densities in  
275 our experiment, rather than exerting extremely strong top-down effects on prey fish  
276 populations. In our experiment, the ratio of prey fish biomass to pike biomass in the  
277 investigated ponds at the end of the experiment averaged circa 4 (large inedible size classes  
278 of common carp excluded), which is comparable to ratios frequently found in other ponds of  
279 the area (Joachim Mergeay and Johan Auwerx, unpublished results).

280 Multiple studies have shown that percids are particularly vulnerable to cormorant predation  
281 (Skov *et al.* 2014; Rudstam *et al.* 2004; Östman *et al.* 2012). Both the use of artificial refuges  
282 by perch and reduced predation losses of perch in the presence of artificial refuges have  
283 previously been demonstrated in short-term experiments (Russell *et al.* 2008; Russell *et al.*  
284 2003). Nevertheless, we were unable to demonstrate such beneficial effects on perch in our  
285 experiment. It should be noted, however, that perch densities were highly variable between  
286 ponds, most probably due to relatively low initial stocking densities combined with a high  
287 variability in reproduction success among ponds. Such large variation may have  
288 overwhelmed any refuge effect. Although we were not able to demonstrate refuge effects  
289 for this species, it would be unsafe to conclude on the basis of our results that the potential  
290 of artificial refuges to protect perch is low. Similarly, we observed no effect of artificial  
291 refuges on common carp. This observation likely resulted from the high somatic growth  
292 rates of this species, which enabled it to outgrow the vulnerable prey size range already  
293 after the first summer of the experiment (average standard length of common carp in  
294 autumn 2009 = 23 cm, data not shown). The absence of refuge effects on pike likely results  
295 from their territorial ambush predator behavior (Craig 2008), which may reduce collective  
296 use of refuges by pike and can thus limit the effectiveness of artificial refuges for this  
297 species.

298 Artificial refuges had no effects on environmental pond conditions, except that they seem to  
299 have reduced the rate of decline of macrophytes in the second year of the experiment. The  
300 mechanism responsible for this remains unclear. One possibility might be that artificial  
301 refuges favored macrophytes by reducing wind-induced water turbulence (Bornette &  
302 Puijalon 2011). Protection of vegetation from herbivorous birds by refuges cannot have been  
303 a reason because no macrophytes were found to grow within refuges. It is unlikely that the

304 positive effect of refuges on submerged vegetation has been responsible for the observed  
305 refuge effect on planktivorous cyprinids in our experiment. We specified macrophyte cover  
306 as a covariable in our analyses and as such accounted for it. In addition, we found no  
307 evidence for any effect of submerged vegetation on fish biomass, with the exception of a  
308 positive effect on pike. Therefore, our study indicates that artificial refuges do effectively  
309 protect rudd and roach populations against predation by cormorants in the presence of  
310 aquatic vegetation. The absence of macrophyte effects on the majority of fish species in our  
311 experiment may also result from a more pronounced cormorant predation during the winter  
312 period when vegetation is absent and ponds are visited more frequently by cormorants  
313 (pers. observation). We argue that artificial refuges may be particularly valuable during  
314 winter periods when aquatic vegetation is absent.

315 In conclusion, the results of our pond experiment provide strong evidence for positive  
316 effects of artificial refuges on populations of rudd and roach. The use of artificial refuges of  
317 the type used by us and earlier work (Russell *et al.* 2008) may therefore be an effective and  
318 sustainable method to facilitate the coexistence of predation vulnerable fish populations  
319 with cormorants in ponds and shallow lakes. However, it is important to realize that the  
320 efficiency of the refuges is highly species-specific and seems to depend on the characteristics  
321 of the fish community. We argue that artificial refuges can be a valuable alternative to the  
322 suppression of cormorant populations by hunting, a practice that has recently been shown  
323 to be ineffective on the longer time (Bregnballe *et al.* 2015; Chamberlain *et al.* 2013). Finally,  
324 our results provide circumstantial evidence that the presence of refuges themselves may  
325 promote vegetation cover.

326

327 **REFERENCES**

- 328 Barks P.M., Doucette J.L. & Somers C.M. (2010) Lack of angling-sized yellow perch in a Canadian  
 329 boreal lake: potential influences of growth rate, diet, and predation by double-crested  
 330 cormorants. *Transactions of the American Fisheries Society*, **139**, 1029-1040.
- 331 Berg S., Jeppesen E. & Søndergaard M. (1997) Pike (*Esox lucius* L.) stocking as a biomanipulation tool  
 332 1. Effects on the fish population in Lake Lyng, Denmark. *Hydrobiologia*, **342**, 311-318.
- 333 Borcard D., Gillet F. & Legendre P. (2011) *Numerical Ecology with R*. New York: Springer, 306 pp.
- 334 Bornette G. & Puijalon S. (2011) Response of aquatic plants to abiotic factors: a review. *Aquatic  
 335 Sciences*, **73**, 1-14.
- 336 Bregnballe T., Hyldgaard A.M., Clausen K.K. & Carss D.N. (2015) What does three years of hunting  
 337 great cormorants, *Phalacrocorax carbo*, tell us? Shooting autumn-staging birds as a means of  
 338 reducing numbers locally. *Pest Management Science*, **71**, 173-179.
- 339 Bugajski A., Reudink M.W., Doucette J.L., Franks S.E., Wissel B., Somers C.M. *et al.* (2012) The  
 340 complexity of cormorants: stable isotopes reveal multiple prey sources and feeding site  
 341 switching. *Canadian Journal of Fisheries and Aquatic Sciences*, **70**, 271-279.
- 342 Carss D.N., Bell S. & Marzano M. (2009) Competing and coexisting with cormorants. In: S. Heckler  
 343 (ed) *Landscape, process and power: re-evaluating traditional environmental knowledge*. New  
 344 York: Berghahn Books, 99-121 pp.
- 345 Casaux R.J., Prinzie C.Y.D., Bertolin M.L. & Tartara M.A. (2009) Diet of the Neotropic Cormorant  
 346 *Phalacrocorax olivaceus* at West Chubut, Patagonia, Argentina. *Waterbirds*, **32**, 444-449.
- 347 Chamberlain D., Austin G., Newson S., Johnston A. & Burton N. (2013) Licensed control does not  
 348 reduce local Cormorant *Phalacrocorax carbo* population size in winter. *Journal of  
 349 Ornithology*, **154**, 739-750.
- 350 Cosolo M., Ferrero E.A. & Sponza S. (2010) Prey ecology and behaviour affect foraging strategies in  
 351 the Great Cormorant. *Marine biology*, **157**, 2533-2544.
- 352 Craig J. (2008) A short review of pike ecology. *Hydrobiologia*, **601**, 5-16.
- 353 Dalton C.M., Ellis D. & Post D.M. (2009) The impact of double-crested cormorant (*Phalacrocorax  
 354 auritus*) predation on anadromous alewife (*Alosa pseudoharengus*) in south-central  
 355 Connecticut, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, **66**, 177-186.
- 356 Devos K., Vermeersch G. & Anselin A. (2011) Populatieontwikkeling van Aalscholvers in Vlaanderen,  
 357 periode 2009-2011. *Vogelnieuws*. Brussel: Instituut voor Natuur- en Bosonderzoek, pp. 4-21.
- 358 Diana J.S., Maruca S. & Low B. (2006) Do increasing cormorant populations threaten sportfishes in  
 359 the Great Lakes? A case study in Lake Huron. *Journal of Great Lakes Research*, **32**, 306-320.
- 360 Dirksen S., Boudewijn T.J., Noordhuis R. & Marteiijn E.C.L. (1995) Cormorants *Phalacrocorax carbo  
 361 sinensis* in shallow eutrophic freshwater lakes: prey choice and fish consumption in the non-  
 362 breeding period and effects of large-scale fish removal. *Ardea*, **83**, 167-184.
- 363 Doucette J.L., Wissel B. & Somers C.M. (2011) Cormorant–fisheries conflicts: Stable isotopes reveal a  
 364 consistent niche for avian piscivores in diverse food webs. *Ecological Applications*, **21**, 2987-  
 365 3001.
- 366 Draulans D. (1987) The effect of prey density on foraging behaviour and succes of adult and first-year  
 367 Grey Herons (*Ardea cinerea*). *Journal of Animal Ecology*, **56**, 479-493.
- 368 Eisenhower M.D. & Parrish D.L. (2009) Double-Crested Cormorant and Fish Interactions in a Shallow  
 369 Basin of Lake Champlain. *Waterbirds*, **32**, 388-399.
- 370 Ellner S.P., McCauley E., Kendall B.E., Briggs C.J., Hosseini P.R., Wood S.N. *et al.* (2001) Habitat  
 371 structure and population persistence in an experimental community. *Nature*, **412**, 538-543.
- 372 Emmrich M. & Düttmann H. (2011) Seasonal shifts in diet composition of Great Cormorants  
 373 *Phalacrocorax carbo sinensis* foraging at a shallow eutrophic inland lake. *Ardea*, **99**, 207-216.
- 374 Engström H. (2001) Long term effects of cormorant predation on fish communities and fishery in a  
 375 freshwater lake. *Ecography*, **24**, 127-138.



- 376 Feltham M.J., Davies J.M., Wilson B.R., Holden T., Cowx I.G. & Harvey J.P. (1999) Case Studies of the  
377 Impact of Fish-eating Birds on Inland Fisheries in England and Wales. London: Ministry of  
378 Agriculture, Fisheries and Food. 406 pp.
- 379 Grémillet D., Argentin G., Schulte B. & Culik B.M. (1998) Flexible foraging techniques in breeding  
380 Cormorants *Phalacrocorax carbo* and Shags *Phalacrocorax aristotelis*: benthic or pelagic  
381 feeding? *Ibis*, **140**, 113-119.
- 382 Grémillet D. & Wilson R.P. (1999) A life in the fast lane: energetics and foraging strategies of the  
383 great cormorant. *Behavioral Ecology*, **10**, 516-524.
- 384 Grémillet D., Wilson R.P., Storch S. & Gary Y. (1999) Three-dimensional space utilization by a marine  
385 predator. *Marine Ecology Progress Series*, **183**, 263-273.
- 386 Jacobsen L. & Perrow M.R. (1998) Predation risk from piscivorous fish influencing the diel use of  
387 macrophytes by planktivorous fish in experimental ponds. *Ecology of Freshwater Fish*, **7**, 78-  
388 86.
- 389 Kloskowski J. (2011) Human–wildlife conflicts at pond fisheries in eastern Poland: perceptions and  
390 management of wildlife damage. *European journal of wildlife research*, **57**, 295-304.
- 391 Koroleff F. (1970) Determination of total phosphorus in natural waters by means of persulphate  
392 oxidation. *Interlaboratory report No. 3, Le Conseil International pour l'exploration de la mer*  
393 *ICES, Pap. CM 1969/C.8, 1970 (1969–1970)*. 54 pp.
- 394 Kumada N., Arima T., Tsuboi J.-i., Ashizawa A. & Fujioka M. (2013) The multi-scale aggregative  
395 response of cormorants to the mass stocking of fish in rivers. *Fisheries research*, **137**, 81-87.
- 396 Lekuona J.M. (2002) Food intake, feeding behaviour and stock losses of cormorants, *Phalacrocorax*  
397 *carbo*, and grey herons, *Ardea cinerea*, at a fish farm in Archachon Bay (Southwest France)  
398 during breeding and non-breeding season. *Folia Zool.*, **51**, 23-34.
- 399 Lepš J. & Šmilauer P. (2003) *Multivariate Analysis of Ecological Data using CANOCO*. New York:  
400 Cambridge University Press, 373 pp.
- 401 Marzano M., Carss D. & Cheyne I. (2013) Managing European cormorant-fisheries conflicts:  
402 problems, practicalities and policy. *Fisheries Management and Ecology*, **20**, 401-413.
- 403 McKay H.V., Russell I.C., Rehfish M.M., Armitage M., Packer J. & Parrot D. (2003) Pilot trials to assess  
404 the efficacy of fish refuges in reducing the impact of cormorants on inland fisheries. In: I.G.  
405 Cowx (ed) *Interactions between fish and birds: Implications for management*. Hull: Hull  
406 International Fisheries Institute, University of Hull, 278-287 pp.
- 407 Nelson J.B. (2005) *Pelicans, cormorants, and their relatives*. Oxford: Oxford University Press, 680 pp.
- 408 Orpwood J.E., Miles M.S., Russell I.C. & Armstrong J.D. (2010) Efficacy of artificial shelters for roach,  
409 *Rutilus rutilus*, against predators in the presence of reeds. *Fisheries Management and*  
410 *Ecology*, **17**, 356-365.
- 411 Östman Ö., Bergenius M., Boström M.K., Lunneryd S.-G. & Sprules W.G. (2012) Do cormorant  
412 colonies affect local fish communities in the Baltic Sea? *Canadian Journal of Fisheries and*  
413 *Aquatic Sciences*, **69**, 1047-1055.
- 414 Prejs A., Martyniak A., Boroń S., Hliwa P. & Koperski P. (1994) Food web manipulation in a small,  
415 eutrophic Lake Wirbel, Poland: effect of stocking with juvenile pike on planktivorous fish.  
416 *Hydrobiologia*, **275**, 65-70.
- 417 Putman R. (1994) *Community Ecology*. London: Chapman and Hall, 178 pp.
- 418 Rudstam L.G., Van De Valk A.J., Adams C.M., Coleman J.T.H., Forney J.L. & Richmond M.E. (2004)  
419 Cormorant Predation and the Population Dynamics of Walleye and Yellow Perch in Oneida  
420 Lake. *Ecological Applications*, **14**, 149-163.
- 421 Russell I., Broughton B., Keller T. & Carss D. (2012) The INTERCAFE Cormorant Management Toolbox,  
422 Methods for reducing Cormorant problems at European fisheries. 85 pp.
- 423 Russell I., Parrott D., Ives M., Goldsmith D., Fox S., Clifton-Dey D. *et al.* (2008) Reducing fish losses to  
424 cormorants using artificial fish refuges: an experimental study. *Fisheries Management and*  
425 *Ecology*, **15**, 189-198.

- 426 Russell I.C., Dare P.J., Eaton D.R. & Armstrong J.D. (1996) Assessment of the Problem of Fish-Eating  
427 Birds in Inland Fisheries in England and Wales. Report to the Ministry of Agriculture, Fisheries  
428 and Food. MAFF Project VC 0104. 48 pp.
- 429 Russell I.C., Dare P.J., Mc Kay H.V. & Ives S.J. (2003) The potential for using fish refuges to reduce  
430 damage to inland fisheries by cormorants, *Phalacrocorax carbo*. In: I.G. Cowx (ed)  
431 *Interactions between fish and birds: Implications for management*. Hull, UK: Hull  
432 International Fisheries Institute, University of Hull, pp. 259-277.
- 433 Salmi J.A., Auvinen H., Raitaniemi J., Kurkilahti M., Lilja J. & Maikola R. (2015) Perch (*Perca fluviatilis*)  
434 and pikeperch (*Sander lucioperca*) in the diet of the great cormorant (*Phalacrocorax carbo*)  
435 and effects on catches in the Archipelago Sea, Southwest coast of Finland. *Fisheries Research*,  
436 **164**, 26-34.
- 437 Santoul F., Hougas J.-B., Green A.J. & Mastroiello S. (2004) Diet of great cormorants *Phalacrocorax*  
438 *carbo sinensis* wintering in Malaucène (South-West France). *Archiv für Hydrobiologie*, **160**, 281-  
439 287.
- 440 Skov C., Jepsen N., Baktoft H., Jansen T., Pedersen S. & Koed A. (2014) Cormorant predation on PIT-  
441 tagged lake fish. *Journal of Limnology*, **73**, 177-186.
- 442 Steffens W. (2010) Great cormorant—substantial danger to fish populations and fishery in Europe.  
443 *Bulgarian Journal of Agricultural Science*, **16**, 322-331.
- 444 Suter W. (1997) Roach rules: shoaling fish are a constant factor in the diet of cormorants  
445 *Phalacrocorax carbo*. Switzerland. *Ardea*, **95**, 9-27.
- 446 Troynikov V., Whitten A., Gorfine H., Pütys Ž., Jakubavičiūtė E., Ložys L. *et al.* (2013) Cormorant Catch  
447 Concerns for Fishers: Estimating the Size-Selectivity of a Piscivorous Bird. *PLoS ONE*, **8**,  
448 e77518.
- 449 Winfield I.J., Crawshaw D.H. & Durie N.C. (2002) Management of the cormorant, *Phalacrocorax*  
450 *carbo*, and endangered whitefish, *Coregonus lavaretus*, populations of Haweswater, UK. In:  
451 I.G. Cowx (ed) *Interactions between fish and birds: Implications between fish and birds:*  
452 *Implications for management*. London: Fishing News Books, 335-344 pp.
- 453 Young J., Marzano M., White R., McCracken D., Redpath S., Carss D. *et al.* (2010) The emergence of  
454 biodiversity conflicts from biodiversity impacts: characteristics and management strategies.  
455 *Biodiversity and Conservation*, **19**, 3973-3990.
- 456 Žydelis R. & Kontautas A. (2008) Piscivorous birds as top predators and fishery competitors in the  
457 lagoon ecosystem. *Hydrobiologia*, **611**, 45-54.

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465 **TABLES**

466 Table 1. Median standard length and stocked biomass (kg ha<sup>-1</sup>) for each species for the  
 467 different fish community treatments. (PL) planktivores; (B) benthivores; (PL+B) planktivores  
 468 and benthivores; (PL+B+PI) planktivores, benthivores and piscivores.

	median size (min.- max.)	PL	B	PL+B	PL+B+PI
Roach ( <i>Rutilus rutilus</i> L.)	16.3 cm (7.0 - 23.0)	43	0	21	21
Rudd ( <i>Scardinius erythrophthalmus</i> L.)	12.0 cm (9.0 - 21.0)	43	0	21	21
Perch ( <i>Perca fluviatilis</i> L.)	9.5 cm (8.5 - 13.5)	4	0	3	3
Ide ( <i>Leuciscus idus</i> L.)	8.5 cm (7.5 - 9.5)	10	0	5	5
Common carp ( <i>Cyprinus carpio</i> L.)	11.5 cm (9.5 - 14)	0	100	50	50
Pike ( <i>Esox lucius</i> L.) *	9 cm (7 - 13)	0	0	0	0.63
Total fish biomass		100	100	100	100.63

\* pike was stocked as fingerlings (150 ind ha<sup>-1</sup>, mean individual body weight = 4.2 gr)

469  
 470 Table 2. RDA results for the effect of fish, refuges and the interaction between both on the  
 471 investigated environmental pond characteristics (suspended solids, conductivity, alkalinity,  
 472 chlorophyll *a* concentration, pH, water transparency, day-time oxygen concentration, and  
 473 coverage with submerged and emergent vegetation) in 2009 and 2010. Significant *P* values  
 474 are shown in bold.

		<i>R</i> <sup>2</sup> (%)	<i>F</i>	<i>P</i>
2009	Fish	15.1	1.08	0.387
	Refuges	1.3	0.28	0.932
	Fish*Refuges	15.6	0.83	0.652
2010	Fish	12.6	1.00	0.455
	Refuges	11.5	2.72	<b>0.048</b>
	Fish*Refuges	0.2	1.33	0.216

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480 Table 3. Results of ANCOVA analyses testing for the effect of fish treatment, the presence of  
 481 artificial refuges, the interaction between fish treatment and refuges, and the percentage of  
 482 submerged vegetation cover on the biomass of each stocked species separately. Significant *P*  
 483 values are shown in bold.

	SS	df	MS	F	P
Planktivorous cyprinids (adults)					
Fish	0.0483	2	0.0242	0.27	0.765
Refuges	0.6819	1	0.6819	7.73	<b>0.018</b>
Fish*Refuges	0.2956	2	0.1478	1.68	0.232
Submerged vegetation cover	0.0459	1	0.0459	0.52	0.486
Error	0.9702	11	0.0882		
Planktivorous cyprinids (Y1Y)					
Fish	1.7844	2	0.8922	1.42	0.284
Refuges	2.3935	1	2.3935	3.80	0.077
Fish*Refuges	2.3753	2	1.1876	1.88	0.198
Submerged vegetation cover	0.6133	1	0.6133	0.97	0.345
Error	6.9335	11	0.6303		
Planktivorous cyprinids (YOY)					
Fish	0.3065	2	0.1532	0.72	0.508
Refuges	1.3476	1	1.3476	6.34	<b>0.029</b>
Fish*Refuges	1.5359	2	0.768	3.61	0.062
Submerged vegetation cover	0.0145	1	0.0145	0.07	0.799
Error	2.3395	11	0.2127		
Perch					
Fish	0.1864	2	0.0932	0.22	0.805
Refuges	0.0205	1	0.0205	0.05	0.829
Fish*Refuges	0.1202	2	0.0601	0.14	0.868
Submerged vegetation cover	0.6228	1	0.6228	1.48	0.249
Error	4.6276	11	0.4207		
Ide					
Fish	0.5659	2	0.2829	1.17	0.346
Refuges	0.5263	1	0.5263	2.18	0.168
Fish*Refuges	0.4947	2	0.2473	1.02	0.391
Submerged vegetation cover	0.0045	1	0.0045	0.02	0.894
Error	2.6558	11	0.2414		
Common carp					
Fish	0.4416	2	0.2208	1.51	0.264
Refuges	0.3265	1	0.3265	2.23	0.164
Fish*Refuges	0.1783	2	0.0892	0.61	0.562
Submerged vegetation cover	0.0027	1	0.0027	0.02	0.894
Error	1.6124	11	0.1466		
Pike					
Refuges	0.0236	1	0.0236	2.06	0.247
Submerged vegetation cover	0.1642	1	0.1642	14.33	<b>0.032</b>
Error	0.0344	3	0.0115		

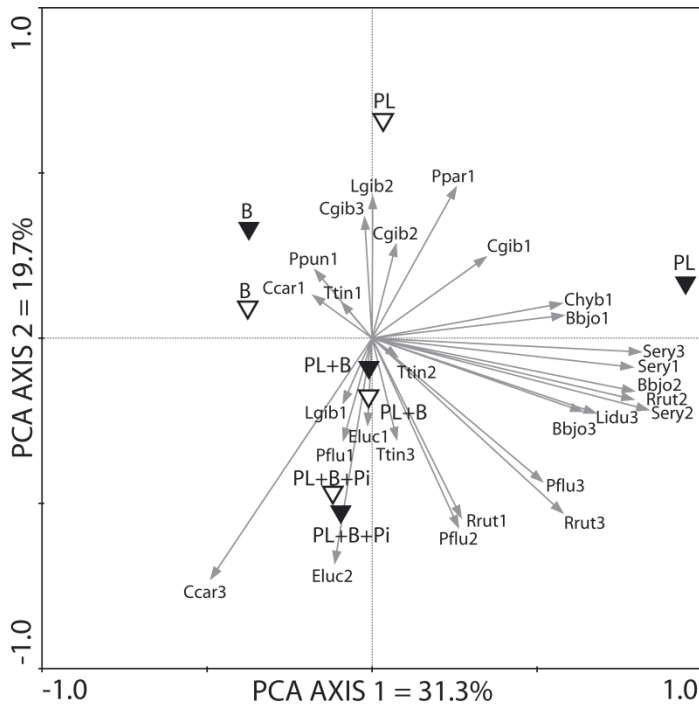
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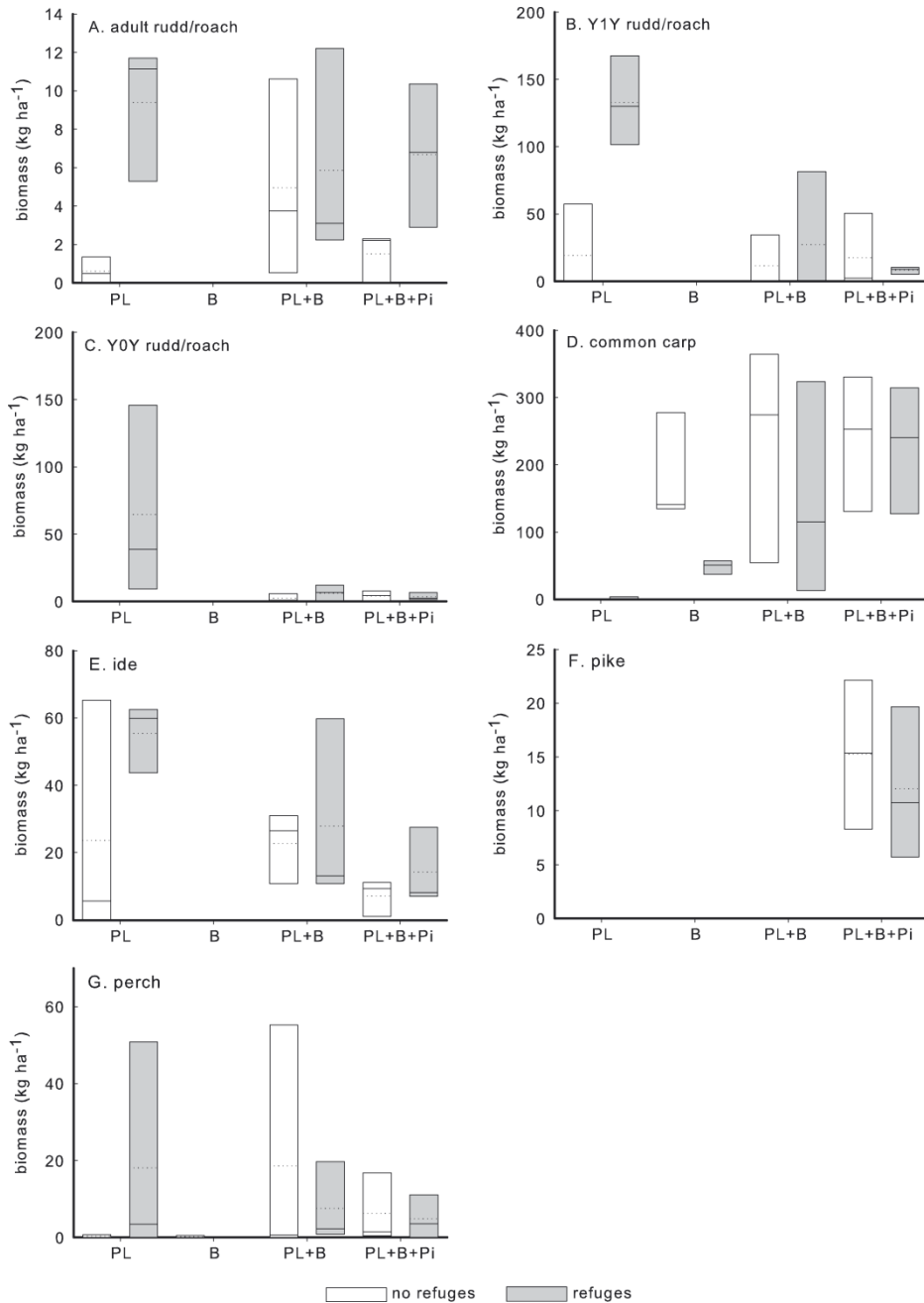
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488 **FIGURES**



489  
 490 Figure 1. Biplot of Principal Component Analysis (PCA) representing the association between  
 491 fish species and fish treatment (PL = planktivores, B = benthivores, PL+B = planktivores +  
 492 benthivores, PL+B+Pi= planktivores + benthivores + piscivores) in the presence and absence  
 493 of artificial refuges (black and white triangles respectively). Triangles represent the centroids  
 494 of the experimental treatments and do not influence the ordination. Arrows represent the  
 495 linear responses of fish species and their size classes. The numbers behind the species  
 496 abbreviations indicate the different age cohorts (see Table S3. for full species names and the  
 497 distinguished age classes).

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500 Figure 2. Boxplots with the median (solid line) and the average (dotted line) of the total  
 501 biomass for each stocked fish species separately at the end of the experiment in the  
 502 presence and absence of artificial refuges. PL= planktivorous fish treatment, B= benthivorous  
 503 fish treatment, PL+B= combination of planktivores and benthivores, PL+B+Pi= combination  
 504 of planktivores, benthivores and piscivores. Boxes represent the 25<sup>th</sup> and 75<sup>th</sup> percentile.

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507 **SUPPORTING INFORMATION**

508 **SI 1. Detailed information on the fish community characteristics in the experiment ponds.**

509 The initial fish stock treatment significantly determined fish community composition ( $R^2 =$   
510 41.4%,  $F = 4.617$ ,  $P = 0.005$ ) at the end of the experiment. Fish biomasses in the ponds  
511 averaged 245 kg ha<sup>-1</sup> at the end of the experiment (Fig. S4). The majority of ponds (n=17)  
512 contained a fraction of non-stocked fish species, in which topmouth gudgeon  
513 (*Pseudorasbora parva* Temminck & Schlegel) was numerically dominant, but also gibel carp  
514 (*Carassius gibelion* Bloch), pumpkinseed sunfish (*Lepomis gibbosus* L.), tench (*Tinca tinca* L.),  
515 silver bream (*Blicca bjoerkna* L.) and brown bullhead (*Ameirus nebulosus* Lesueur) were  
516 observed. These fishes may have passed the fine mesh at the inlets as juveniles during  
517 refilling the ponds prior to the experiment, but may in some cases also have survived the  
518 winter in small puddles and pools that remained after drainage in some ponds. Populations  
519 of stocked planktivorous cyprinids (rudd and roach) had reproduced successfully in both  
520 years and their populations were characterized by a considerable fraction of young of the  
521 year (YOY) and one year old fish (Y1Y) (on average 16.27 % and 44.30 % of total population  
522 biomass, respectively). We found evidence for reproduction of perch in 12 of the 19 ponds  
523 that had been stocked with this species, but biomasses of juvenile perch in these ponds  
524 were highly variable (min., max. and median biomass of juveniles 0.01 kg.ha<sup>-1</sup>, 51.65 kg ha<sup>-1</sup>  
525 and 1.73 kg ha<sup>-1</sup>, respectively). Ide increased in body size and overall population biomass  
526 (mean SL = 21.2 cm, mean population biomass 25.11 kg ha<sup>-1</sup>), but the species did not  
527 reproduce during the experiment. Populations of common carp and pike were characterized  
528 by a strong increase in biomass (mean population biomass at the end of the experiment  
529 182.65 kg ha<sup>-1</sup> and 14.33 kg ha<sup>-1</sup>, respectively) and high somatic growth (mean SL of adult

530 common carp and pike at the end of the experiment 28.1 cm and 32.9 cm, respectively).

531 Both species reproduced in one pond in 2010.

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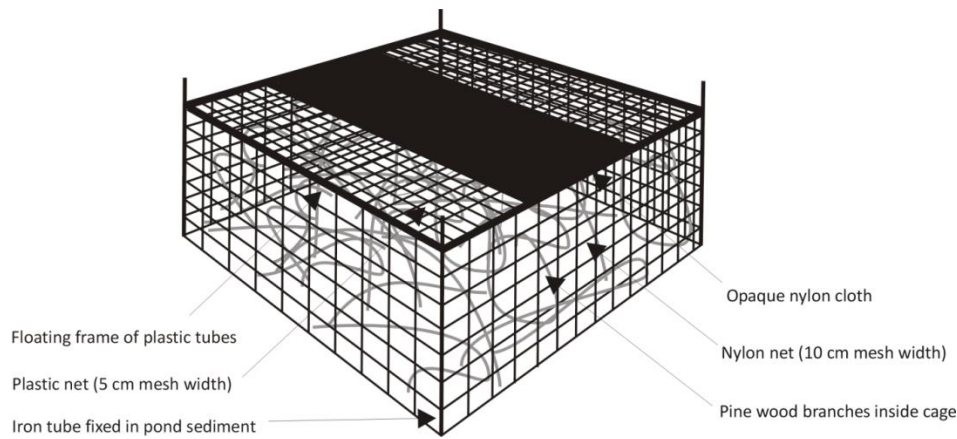
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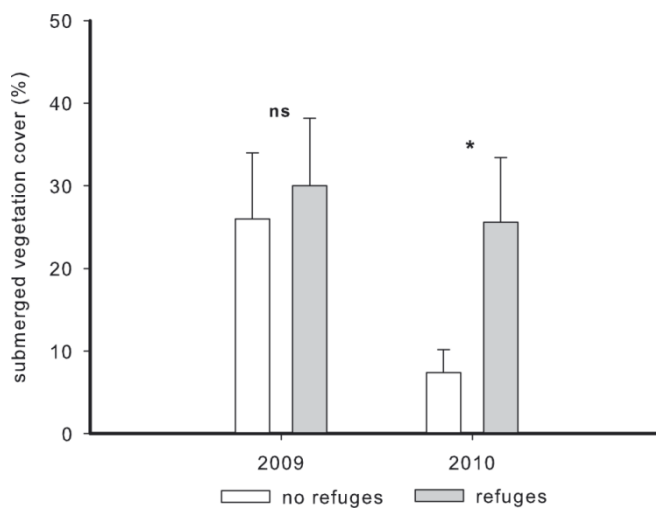


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551 Figure S1. A schematic overview of the structure of the artificial refuges. The top frame  
552 floats on the water surface and follows the natural variation in water level. The four sides of  
553 the refuges are closed with nylon nets and encompass the entire water column. We covered  
554 1/3<sup>rd</sup> of the upper part with opaque nylon cloth and created internal structure using pine  
555 wood branches. The number of refuges per pond was chosen such that they covered  
556 approximately 5% of the total pond surface.

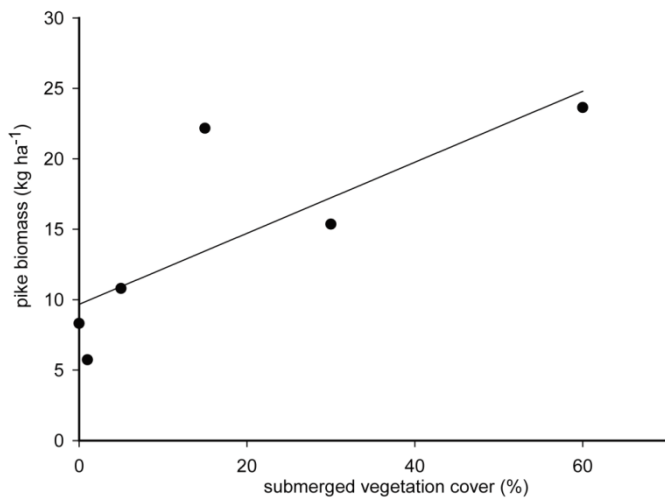
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559 Figure S2. Mean percentage of coverage with submerged vegetation in 2009 and 2010 in the  
560 absence and presence of refuges (white and grey bars respectively). Error bars denote the  
561 standard error of the mean (ns: not significant, \*Kruskal-Wallis test:  $P < 0.05$ ).

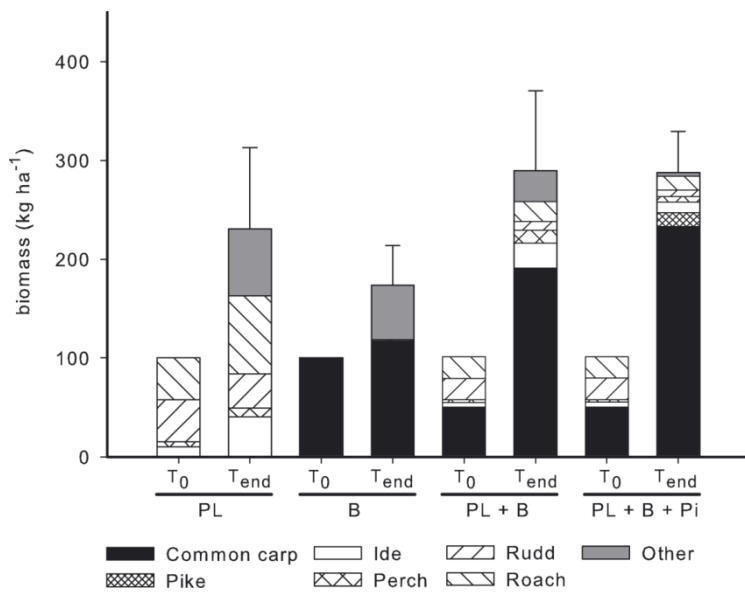
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564 Figure S3. Association between percentage of pond surface covered by submerged  
 565 vegetation and pike community biomass (Spearman rank correlation,  $r = 0.88$ ,  $P = 0.033$ ).

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568 Figure S4. Mean total fish biomass and species composition at the start ( $T_0$ ) and end ( $T_{end}$ ) of  
 569 the experiment for the different fish stock treatments. PL= planktivorous fish only, B=  
 570 benthivorous fish only, PL+B= planktivores and benthivores, PL+B+Pi= planktivores,  
 571 benthivores and piscivores. Error bars show the standard error of the mean total fish  
 572 biomass.

573 Table S1. Common names and scientific names of all fish species in this study and their body  
 574 size ranges.

code	scientific name	name	body size *
Aneb1	<i>Ameiurus nebulosus</i>	Brown bullhead	7-18
Bbjo1	<i>Blicca bjoerkna</i>	Silver bream	0-8
Bbjo2	<i>Blicca bjoerkna</i>	Silver bream	8-12
Bbjo3	<i>Blicca bjoerkna</i>	Silver bream	>12
Ccar1	<i>Cyprinus carpio</i>	Common carp	0-10
Ccar3	<i>Cyprinus carpio</i>	Common carp	>18
Cgib1	<i>Carassius gibelio auratus</i>	Gibel carp	0-6
Cgib2	<i>Carassius gibelio auratus</i>	Gibel carp	6-10
Cgib3	<i>Carassius gibelio auratus</i>	Gibel carp	<10
Chyb1	-	Gibel hybrid	0-6
Eluc1	<i>Esox lucius</i>	Pike	0-18
Eluc2	<i>Esox lucius</i>	Pike	>18
Lgib1	<i>Lepomis gibbosus</i>	Pumpkinseed sunfish	0-4.8
Lgib2	<i>Lepomis gibbosus</i>	Pumpkinseed sunfish	>4,8
Lidu3	<i>Leusiscus idus</i>	Pumpkinseed sunfish	16-30
Pflu1	<i>Perca fluviatilis</i>	Perch	0-7
Pflu2	<i>Perca fluviatilis</i>	Perch	7-12
Pflu3	<i>Perca fluviatilis</i>	Perch	>12
Ppar1	<i>Pseudorasbora parva</i>	Topmouth gudgeon	all sizes
Ppun1	<i>Pungitius pungitius</i>	Ninespine stickleback	all sizes
Rrut1	<i>Rutilus rutilus</i>	Roach	0-9
Rrut2	<i>Rutilus rutilus</i>	Roach	9-15
Rrut3	<i>Rutilus rutilus</i>	Roach	>15
Sery1	<i>Scardinius erythrophthalmus</i>	Rudd	0-7
Sery2	<i>Scardinius erythrophthalmus</i>	Rudd	7-13
Sery3	<i>Scardinius erythrophthalmus</i>	Rudd	>13
Ttin1	<i>Tinca tinca</i>	Tench	0-7
Ttin2	<i>Tinca tinca</i>	Tench	7-13
Ttin3	<i>Tinca tinca</i>	Tench	>13

575 \* standard length in cm

576