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

Pieter Lemmens^{1*}, Luc De Meester¹ and Steven A.J. Declerck²

¹ Laboratory of Aquatic Ecology, Evolution and Conservation, KU Leuven, Ch. Deberiotstraat 32, 3000 Leuven, Belgium;

² Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB Wageningen, The Netherlands.

* Corresponding author: pieter.lemmens@bio.kuleuven.be

ABSTRACT

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

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

INTRODUCTION

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 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 populations in many parts of the world is often considered a great success in terms of nature conservation (Young *et al.* 2010). Yet, their successful comeback fuels conflicts between different stakeholder groups worldwide (Žydelis & Kontautas 2008; Carss *et al.* 2009; Marzano *et al.* 2013; Kloskowski 2011).

Currently, there exists a highly polarized debate on the extent to which cormorants affect fish communities. Multiple investigations show that predation by cormorants has no or only marginal effects on fish communities (Engström 2001; Dalton *et al.* 2009; Barks *et al.* 2010; Östman *et al.* 2012). Other studies suggest that cormorants affect local fish populations negatively (Winfield *et al.* 2002; Rudstam *et al.* 2004; Steffens 2010; Salmi *et al.* 2015). Cormorants have since long been held accountable for considerable economic and socio-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 likely to occur, remains, however, largely unclear (Doucette *et al.* 2011).

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

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

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

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

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

Experimental design

We drained twenty-four former fish farming ponds (ranging in size from 0.239 to 2.224 ha) during autumn 2008 and removed the resident fish communities. The ponds were subsequently refilled in early spring 2009. During refilling, fine mesh stainless steel grids (2 mm) were placed at the inlets to minimize the entrance of wild fish. After filling, all hydrological connections with rivulets and other ponds were closed. We stocked the ponds in early March 2009 with four differently composed fish communities, all with a total initial biomass of 100 kg ha⁻¹. Fish treatments were defined as (1) small planktivorous fish only (adult rudd and roach, one year old ide and small perch, PL); (2) benthivorous fish only (one year old common carp, B); (3) planktivorous and benthivorous fish (50 kg ha⁻¹ of each, PL+B); and (4) planktivores, benthivores and piscivores (pike fingerlings, PL+B+PI). We refer to Table 1 for more details on the stocked fish communities. Each of these fish stock treatments was replicated with six randomly selected ponds. In half of the ponds of each fish treatment (n = 3), we constructed cages meant to act as refuges for fish against cormorant predation. These refuges were constructed following the design of Russell *et al.* (2008) and consisted of cubic frames, covering a surface of 144 m² (Fig. S1). The four sides of the refuges were closed with nylon nets (10 cm mesh width) to make them encompass the entire water column. To enhance the attractiveness of the refuges for fish, we covered 1/3rd of their upper part with an opaque nylon cloth and created internal structure by placing pine wood branches inside each cage. The number of refuges per pond was chosen such that they covered approximately 5% of the total pond surface (cumulative surfaces per pond ranging from 179 to 1197 m²). The experiment lasted almost two years (from early spring 2009 to late autumn 2010) and thus incorporated an entire winter period during which predation pressure by 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

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

Data analysis

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

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

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

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

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

RESULTS

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

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

DISCUSSION

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

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

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

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

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

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

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

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

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

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. & Martelijn 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.

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

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

TABLES

Table 1. Median standard length and stocked biomass (kg ha^{-1}) for each species for the different fish community treatments. (PL) planktivores; (B) benthivores; (PL+B) planktivores 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^{-1} , mean individual body weight = 4.2 gr)

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

		<i>R</i> ² (%)	<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	0.048
	Fish*Refuges	0.2	1.33	0.216

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

	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Planktivorous cyprinids (adults)					
Fish	0.0483	2	0.0242	0.27	0.765
Refuges	0.6819	1	0.6819	7.73	0.018
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	0.029
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	0.032
Error	0.0344	3	0.0115		

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).
498

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

SUPPORTING INFORMATION

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

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

532

533

534

535

536

537

538

539

540

541

542

543

544

545

546

547

548

549

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 1/3rd 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.

558

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: $P < 0.05$).

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

Figure S4. Mean total fish biomass and species composition at the start (T_0) and end (T_{end}) of the experiment for the different fish stock treatments. PL= planktivorous fish only, B= benthivorous fish only, PL+B= planktivores and benthivores, PL+B+Pi= planktivores, benthivores and piscivores. Error bars show the standard error of the mean total fish 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	Ameiurus nebulosus	Brown bullhead	7-18
Bbjo1	Blicca bjoerkna	Silver bream	0-8
Bbjo2	Blicca bjoerkna	Silver bream	8-12
Bbjo3	Blicca bjoerkna	Silver bream	>12
Ccar1	Cyprinus carpio	Common carp	0-10
Ccar3	Cyprinus carpio	Common carp	>18
Cgib1	Carassius gibelio auratus	Gibel carp	0-6
Cgib2	Carassius gibelio auratus	Gibel carp	6-10
Cgib3	Carassius gibelio auratus	Gibel carp	<10
Chyb1	-	Gibel hybrid	0-6
Eluc1	Esox lucius	Pike	0-18
Eluc2	Esox lucius	Pike	>18
Lgib1	Lepomis gibbosus	Pumpkinseed sunfish	0-4.8
Lgib2	Lepomis gibbosus	Pumpkinseed sunfish	>4,8
Lidu3	Leusiscus idus	Pumpkinseed sunfish	16-30
Pflu1	Perca fluviatilis	Perch	0-7
Pflu2	Perca fluviatilis	Perch	7-12
Pflu3	Perca fluviatilis	Perch	>12
Ppar1	Pseudorasbora parva	Topmouth gudgeon	all sizes
Ppun1	Pungitius pungitius	Ninespine stickleback	all sizes
Rrut1	Rutilus rutilus	Roach	0-9
Rrut2	Rutilus rutilus	Roach	9-15
Rrut3	Rutilus rutilus	Roach	>15
Sery1	Scardinius erythrophthalmus	Rudd	0-7
Sery2	Scardinius erythrophthalmus	Rudd	7-13
Sery3	Scardinius erythrophthalmus	Rudd	>13
Ttin1	Tinca tinca	Tench	0-7
Ttin2	Tinca tinca	Tench	7-13
Ttin3	Tinca tinca	Tench	>13

575 * standard length in cm

576