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PRIMARY RESEARCH PAPER

How equally sized piscivorous birds and fish sharing common food resources may reduce possible feeding interactions between them?

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Abstract The diets of sympatric predators may overlap, especially when their body sizes are similar and foraging area is relatively small. It may be also supposed that some differences in their foraging strategies may counteract competitive interactions among them, and therefore be of advantage to these species. To reveal such phenomena the composition of food of cormorant and adult pikeperch was studied in the Dobczyce Reservoir (S Poland) from June to November 2002. The main prey species were the same and the range of prey size was similar for both piscivores. Despite these similarities, the potential for dietary overlap was strongly reduced due to two differences in their foraging patterns: (1) different preferred prey species (cormorants foraged mainly roach, whereas pikeperch selected juvenile percids); (2) different size of simultaneously selected prey (in summer, cormorants selected larger prey, while in autumn larger prey was selected by pikeperch). These differences may be explained by some general features of birds and fishes, which determine the costs to the individual of capturing prey. The observed selection of different prey species and sizes may be also important for the co-occurrence of other piscivorous birds and fishes sharing common food resources.

Keywords *Phalacrocorax carbo* · *Sander lucioperca* · Diet overlap · Prey size · Diet shift · Central Europe

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Introduction

Fish and aquatic birds often exploit similar food resources (Mous et al., 2003) and the resulting potential competition for food between bird and fish species has received considerable attention. Most of these studies have concerned invertebrate food organisms (Eriksson, 1979; Eadie & Keast, 1982; Beattie & Nudds, 1989; Winfield et al., 1992; Winfield & Winfield, 1994; Wagner, 1997; Wagner & Hansson, 1998), and only a few have focused on comparing the diets of piscivorous birds and fishes in the same foraging area and at the same time. Humphries et al. (1992) compared the diets of birds (four species of cormorants: *Phalacrocorax melanocephalus*, *P. sulcirostris*, *P. varius*, and *P. carbo*) and a scorpaeniform fish (the yank flathead, *Platycephalus speculator*) in the Wilson Inlet estuary, Western Australia; Van Eerden et al. (1993) studied exploitation of food resources by the great crested grebe, *Podiceps cristatus* and European perch, *Perca fluviatilis* in Lake IJsselmeer (The Netherlands); and Goldsworthy et al.

(2001) investigated trophic interactions between Patagonian toothfish, *Dissostichus eleginoides*, seabirds and seals around Macquarie Island (southern Pacific Ocean). More recently, Bur et al. (2008) compared the diets of walleye, *Sander vitreus*, and mergansers, *Mergus serrator*, in Lake Erie. The results of these studies provide the opportunity to compare foraging strategies of phylogenetically distant predators sharing common food resources. Such comparisons are especially interesting when the studied species are of similar body size, because their ecological niches are probably closer and the results obtained may supply information concerning the possibility of co-occurrence in potentially competitive relationships. Cormorant, *Phalacrocorax carbo* (L., 1758) and pikeperch, *Sander lucioperca* (L., 1758) comprise a pair of sympatric and equally sized piscivores; however, their feeding patterns have not been previously compared.

Cormorant and pikeperch co-occur in many inland waters of Europe. Both species reach similar body mass (cormorant, 1.8–3.5 kg; pikeperch, although sometimes over 10 kg, most of the adult fraction of a stock ranges within 1–4 kg; Deelder & Willemsen, 1964), and are top piscivorous predators especially common in eutrophic water bodies. Cormorants have rapidly increased in numbers over the last two decades in Western and then in Central Europe (Lindell et al., 1995), probably as a result of both legal protection and an overall increase in fish productivity in European waters due to anthropogenic eutrophication (Van Eerden et al., 1995). In Poland, this increase in numbers has, since the mid-1980s, been accompanied by breeding in the southern parts of the country (Lindell et al., 1995).

Pikeperch is a percid fish fairly abundant in slowly flowing rivers and lakes in Central and Eastern Europe, especially those with low transparency (i.e. of Secchi depth within 1–1.5 m), where it is often the main predatory fish species. Its distribution range is now extending due to introductions for fishery purposes. In addition, within their native range, pikeperch have increased their populations in eutrophic waters and have colonized newly created dam reservoirs (Kubečka, 1993). The fish occurs in waters of all the lowland and submontane parts of Poland.

The cormorant is a diurnal, diving bird that searches, pursues and captures fish underwater (Cramp & Simmons, 1977), while the pikeperch is a large predatory fish that chases prey in open water and is most active during the crepuscular periods (Jepsen et al., 1999; Poulet et al., 2005). Therefore, in larger waterbodies such as lakes, cormorant and pikeperch forage in the same habitats, i.e. in the sparsely vegetated littoral and limnetic zones. In addition, it may be supposed that both select as prey the dominant species in the fish community (Engström & Jonsson, 2003; Russell et al., 2003; Stempniewicz et al., 2003; Keskinen & Marjomäki, 2004; Dörner et al., 2007; Kangur et al., 2007).

The aim of this study was to determine whether the diets of sympatric cormorant and pikeperch overlap, or if they in fact forage on different prey, in a dam reservoir with environmental features typical of reservoirs located in submontane regions of Central Europe. The findings may support a better understanding of the factors influencing the foraging strategies of cormorant and pikeperch in a man-made lake which provides suitable habitat for both species. Conclusions may also be generally relevant to distant taxa of sympatric piscivores.

Study area

The study was carried out on the Dobczyce Reservoir (49°52′N, 20°03′E, altitude 270 m) in 2002. This reservoir is located on the Raba River (a tributary of the Vistula) in southern Poland, about 30 km south of Cracow (Fig. 1). It is a submontane reservoir with an area of 985 ha, volume of 108 GL, shoreline of approximately 42 km, mean depth of 11.0 m (maximum depth reaches 27 m), and mean water residence time of 0.34 yr (Amirowicz, 1998). In general, the littoral zone is narrow because of the relatively steep slopes of the inundated river valley. Aquatic vegetation is scarce due to fluctuations of the water level. The reservoir is usually ice-covered in January and February.

The fish community consists of 19 species. The most abundant are five cyprinid and percid species, i.e. roach *Rutilus rutilus* (L.), bream *Abramis brama* (L.), bleak *Alburnus alburnus* (L.), perch, and pikeperch. White bream *Blicca bjoerkna* (L.), rudd *Scardinius erythrophthalmus* (L.), chub *Leuciscus cephalus* (L.), and ruffe *Gymnocephalus cernuus* (L.) are less abundant, with the remaining 10 species being relatively rare [*Esox lucius* L., *Cyprinus carpio* L.,

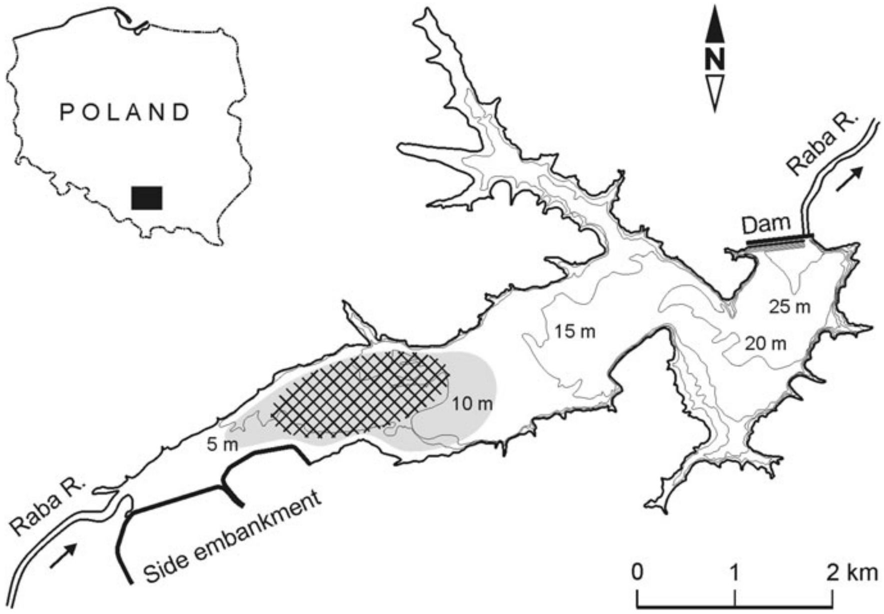

Fig. 1 The foraging area of cormorant *Phalacrocorax carbo* (L.) (*shaded*) and the area of catches of pikeperch *Sander lucioperca* (L.) (*cross-hatched*) in the Dobczyce Reservoir in 2002

Carassius carassius (L.), *C. auratus gibelio* (L.), *Aspius aspius* (L.), *Vimba vimba* (L.), *Chondrostoma nasus* (L.), *Tinca tinca* (L.), *Silurus glanis* L., *Lota lota* (L.)]. The fish biomass in the littoral zone, estimated using shore seining, reached 233 kg ha^{-1} (based only on individuals >20 cm TL; Starzecka et al., 1999). The relative fish density in the limnetic zone, as estimated in hydroacoustic surveys conducted in 2000–2002, was 3,390–5,625 ind. ha^{-1} (individuals >2.8 cm TL; Godlewska & Świerzowski, 2003). According to the equation relating the target strength to fish size provided by Godlewska et al. (2005), this fish density corresponds to a biomass of 61–86 kg ha^{-1}.

The local avifauna is dominated by great crested grebe, mallard, *Anas platyrhynchos* L., and black headed gull, *Larus ridibundus* L. (Gwiazda, 1996). Peak numbers of cormorants are recorded in autumn (max. abundance of >600 ind. was noted on 17 September 2002). There were no cormorant colonies in the vicinity of the reservoir. Numbers in August–October were about 25 times greater than in the March–July period (Gwiazda, 2006).

The main function of the Dobczyce Reservoir is the storage of water for municipal purposes, and so recreation, angling and hunting are banned and all other forms of human activity (including access to the shore) are strictly limited, and therefore the waterfowl are undisturbed. The commercial fishery mainly targets common bream (this species constituted 71–85% of the annual catch in 2000–2002; data of the Regional Water Management Board in Cracow). The fishery activity starts in April and completes in December, with the main fishing gear used being gillnets of 60 mm mesh. Capture of pikeperch and other predatory fishes is avoided as far as possible, according to the biomanipulation concept (only 0.6–0.8 kg of pikeperch per hectare was caught annually as a bycatch in 2000–2002).

Materials and methods

The diet of cormorant was studied by examining regurgitated pellets and stomach contents, while that of pikeperch by stomach content analysis. Fresh pellets were collected from June to November 2002 at a roost located on the southern shore of the reservoir. In addition, the stomach contents of 10 cormorants taken in gillnets in October and November were analysed. All these cormorants were found in gillnets set for bream in the area of the reservoir indicated in Fig. 1. The stomachs of pikeperch were obtained from individuals caught with commercial catches within the area of reservoir used by cormorants for foraging (Fig. 1). The approximate size of this foraging area amounts to about 200 ha. From the available pikeperch, only individuals of body size similar to cormorants (i.e. those within 55–75 cm TL, which corresponds to a body mass of 1.4–3.5 kg) were selected for this analysis. Fish remains were identified and then measured to calculate prey length using published regression formulae (otoliths—Dirksen et al., 1995; pharyngeal bones—Horoszewicz, 1960; chewing pads—Veldkamp, 1995a). The number of individuals of a prey species represented in a pellet was approximated to be the highest total of any of the identifiable parts present, considering right and left parts separately. In the cormorant and pikeperch stomach contents, the number of partially digested prey individuals could in most cases be counted.

In total, 72 pellets with the remains of 282 fishes, and 74 stomachs containing 336 fish, were analysed. In fact, 224 pikeperch were available for stomach content analysis during the study period. However, 103 of them were rejected, because 93 were shorter than 55 cm, and 10 were longer than 75 cm. Of the 121 remaining individuals of appropriate size, 47 had empty stomachs, which amounts to 38.8% of the sample. This collection was divided into three periods, June–July, August–September and October–November, to take into account evidence of seasonal changes in diets. In the first period, 24 pellets and 23 stomachs were examined, while in the second 24 and 19, and in the third 24 and 32, respectively. Among the prey fishes identified to species level, main prey species were categorized as such based on a threshold of forming at least 10% of the total prey number in a period. Remaining species and the individuals identified only to the level of cyprinid or percid family (2.8 and 3.6% in the diets of cormorant and pikeperch, respectively) were pooled as 'others'.

As the statistical analysis was aimed at highlighting similarities or differences in the foraging strategies of the studied piscivores, numbers rather than weights of prey species were compared. It was assumed that the strategy of a piscivore consists of a series of attacks upon individual fish. The attacked fish were selected from an assemblage of all fish of different body size present at a foraging location. This assemblage was composed of a number of species. Thus, the single decision to attack made by a piscivore included both the individual body size and species identity of accessible prey. To assess the importance of a particular prey species in the diet during specific periods, Pielou's (1966) evenness index was used following a rewritten formula (assuming that $J' = H'/H'_{\max}$, where H' is Shannon diversity index, $-\Sigma\, n_i/N \ln n_i/N$, and $H'_{\max} = \ln S$):

$$J' = (N \ln N - \Sigma\, n_i \ln n_i)/(N \ln S)$$

where n_i is the number of ith prey species, N is the total number of prey fish and S is the number of all identified species recorded in the sample. A sample was regarded in this study to be the total number of prey individuals foraged by cormorants or pikeperch during each of three distinct periods. Pielou's index quantifies how even is the composition of the considered assemblage, and can also be used as an index of dominance (as $1 - J'$). Therefore, it may indicate seasonal changes in the dietary composition pattern. Diet overlap between cormorant and pikeperch was evaluated using Morisita's index (Morisita, 1959), following the original formula rewritten in the form:

$$I_{\mathrm{M}} = (2\Sigma n_{\mathrm{C}i} n_{\mathrm{P}i})/\left[(N_{\mathrm{P}}\Sigma n_{\mathrm{C}i}(n_{\mathrm{C}i}-1))/(N_{\mathrm{C}}-1) + (N_{\mathrm{C}}\Sigma n_{\mathrm{P}i}(n_{\mathrm{P}i}-1))/(N_{\mathrm{P}}-1)\right]$$

where $n_{\mathrm{C}i}$, $n_{\mathrm{P}i}$ are the numbers of ith prey species found in the pellets of cormorant or stomachs of pikeperch, and N_{C} and N_{P} are the respective total numbers of recorded prey fish. As a guide to the significance of the observed overlap, the value of 0.6 was adopted following Langton (1982). The significance of any differences between the distributions of prey lengths in cormorant and pikeperch diets was estimated using the Kolmogorov–Smirnov two-sample test (Blalock, 1960).

Results

Prey species composition

Twelve fish species were recorded in the food of cormorant and pikeperch in the Dobczyce Reservoir (Fig. 2). Five of them—roach, bream, perch, pikeperch, and ruffe—constituted the main prey species and contributed 85.8 and 95.5% by numbers of the whole food consumed by cormorant and pikeperch, respectively. In the cormorant diet, the most frequent prey was roach, which on average constituted almost 50% of its prey by number (Fig. 2). The percentage component of this species in the diet decreased during the study period from 80.9% in June–July, 43.2% in August–September, to 28.7% in October–November. Perch and ruffe were

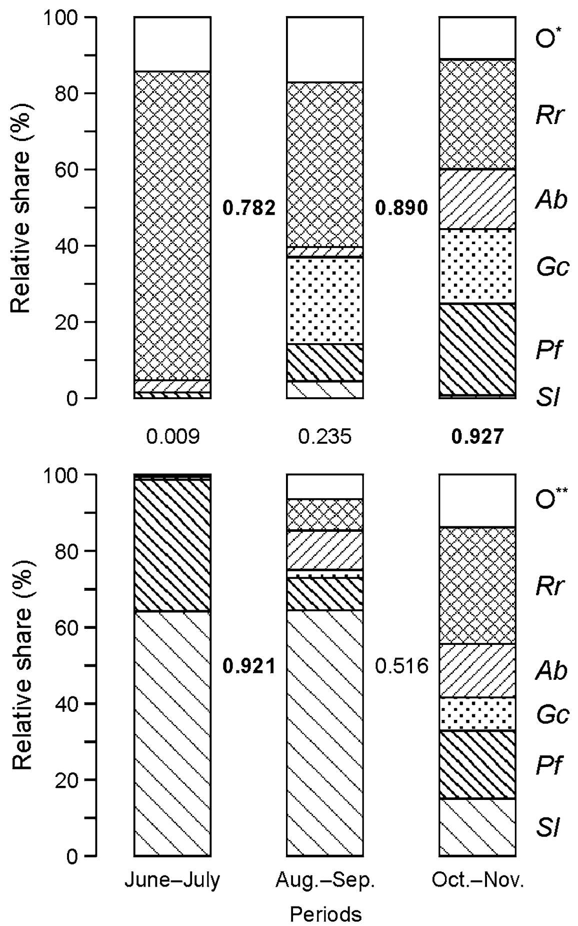

Fig. 2 Fish species composition in the diets of cormorant *Phalacrocorax carbo* (L.) (*upper stacked bar chart*) and pikeperch *Sander lucioperca* (L.) (*lower chart*) in the Dobczyce Reservoir in 2002: *Rr*—*Rutilus rutilus*, *Ab*—*Abramis brama*, *Gc*—*Gymnocephalus cernuus*, *Pf*—*Perca fluviatilis*¸ *Sl*—pikeperch, O—other species (*—*Alburnus alburnus*, *Blicca bjoerkna*, *Cyprinus carpio*, *Leuciscus cephalus*, *L. leuciscus*, *Phoxinus phoxinus*, *Scardinius erythrophthalmus*, **—*A. alburnus*, *B. bjoerkna*) The values of Morisita's index are placed between compared bars (values indicating significant diet overlap are given in *bold*)

also important in cormorant diet, with the exception of the June–July period. The most numerous fish species in cormorant stomachs in October and November were perch (30.0%) and roach (25.0%).

The diet of pikeperch consisted of seven fish species (Fig. 2). The composition of the prey was quite different from that of cormorants at the start of the study because the pikeperch diet was high in juvenile percids at that time. In the first two periods, the young-of-the-year (YOY) pikeperch were the major component of the diet (64.1 and 64.6% in June–July and August–September, respectively) followed by YOY perch (34.4 and 8.3%). In the third period, the cannibalistic behaviour of pikeperch was distinctly reduced (down to 15.2%) while the relative importance of bream and especially roach grew considerably (to 13.9 and 30.4%). The share of ruffe also increased in pikeperch diet in October–November, although this species did not pass the 10% threshold to count as a main prey species.

In general, the contributions of the five most common prey species became more even in both piscivores in the autumn. The evenness of dietary composition increased comparably in cormorant and pikeperch, in respect of both the values of Pielou's index and trend rates. In June–July, the J' index was equal to 0.37 in the diet of cormorant and 0.52 in the diet of pikeperch. The respective figures were 0.67 and 0.63 in August–September, and 0.80 and 0.89 in October–November. This tendency led to a significant dietary overlap in the third 2-month period (Fig. 2). In summer, i.e. in the first two periods, the diets of cormorant and pikeperch were composed of the same prey species, but may be considered as quite different in terms of dietary overlap estimated using Morisita's index, I_M. The I_M values also indicated some differences in the pattern of temporal changes in dietary compositions. In cormorant, the diet changed continuously during the study, as the dietary overlap between consecutive periods was significant. In contrast, the diet of pikeperch remained similar during the first two periods but showed a sharp change in its composition in late summer/early autumn.

Prey length distribution

The range of prey TL in cormorant diet was 3.9–35.1 cm, while the length of fish in the diet of pikeperch ranged between 2.6 and 27.5 cm. Despite these similar ranges of prey size, some distinct differences were found between both species in the first period (Fig. 3). In June–July, prey length distributions were unimodal and considerably skewed towards relatively large fish in cormorant but relatively small fish in pikeperch, with very disparate interquartile ranges of 20.0–25.4 cm and 4.3–5.9 cm, respectively. In the two following periods, the distributions became bimodal and very similar, both in shape and position. The interquartile ranges of prey size in cormorant and pikeperch diets were 7.8–19.6 cm and

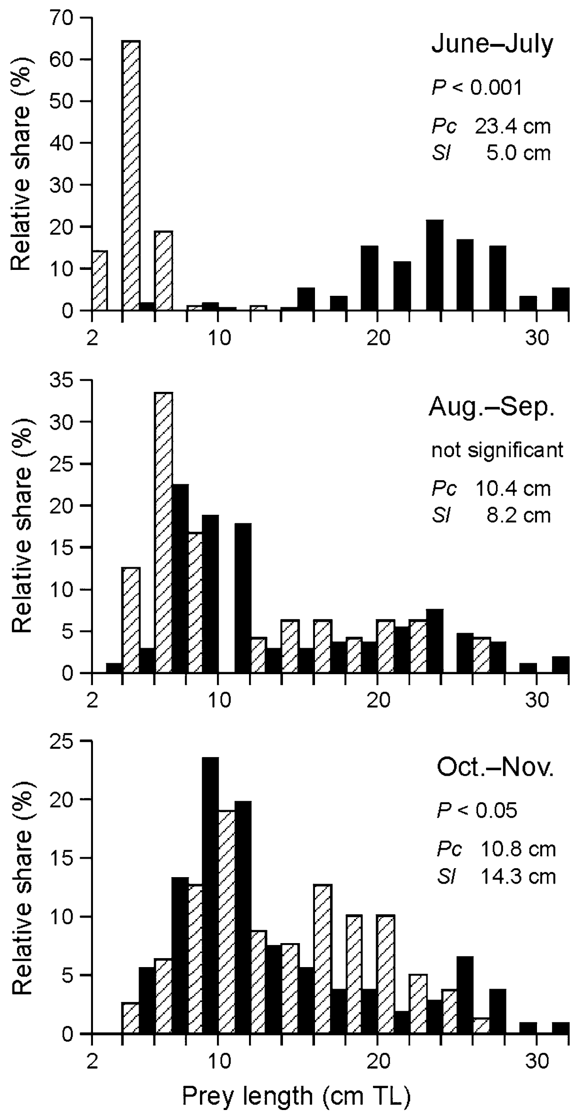

Fig. 3 Frequency distribution of total length of fishes in the diets of cormorant *Phalacrocorax carbo* (L.) (*solid bars*) and pikeperch *Sander lucioperca* (L.) (*hatched bars*) in the Dobczyce Reservoir during three 2-month periods in 2002. In particular periods, the significance levels of differences between presented distributions (*P*; Kolmogorov–Smirnov test) and the median lengths of prey of cormorant (*Pc*) and pikeperch (*Sl*) are given

6.6–16.7 cm in the second period, and 8.2–15.4 cm and 10.4–18.8 cm in the third period, respectively. In general, a peak was located in the approximate range of 6–12 cm, and a band of considerably increased relative share occurred within the length range of 15–25 cm in each size distribution of prey of both piscivores in these two periods (Fig. 3).

The length distributions of particular prey species, especially of the dominant prey species, followed the above patterns. The size of roach foraged by cormorants was distinctly greater in June–July (median = 23.8 cm, Q_1 = 20.0 cm, Q_3 = 25.7 cm) and smaller and the same in the next two periods (median = 10.2 cm, Q_1 = 9.0 cm, Q_3 = 18.7 cm in August–September, and median = 10.2 cm, Q_1 = 8.9 cm, Q_3 = 12.2 cm in October–November). The total lengths of YOY pikeperch dominating the diet of pikeperch were small in June–July (median = 5.3 cm, Q_1 = 4.5 cm, Q_3 = 6.2 cm) and August–September (median = 7.6 cm, Q_1 = 6.5 cm, Q_3 = 8.3 cm), but considerably greater in October–November (median = 19.2 cm, Q_1 = 17.8 cm, Q_3 = 23.0 cm). It should be stressed that, although the size of cormorant prey may be underestimated because diagnostic skeletal elements can be damaged by gastric acids, the obtained differences between the two studied predators were distinct and could not be explained by this effect. The median of total length of fish in the stomachs of cormorants found in gillnets in October and November (12.9 cm; Q_1 = 8.7 cm, Q_3 = 14.0 cm) was similar to the current median value from pellets (10.8 cm; Q_1 = 8.2 cm, Q_3 = 15.4 cm).

Discussion

The results obtained showed that the diets of cormorant and pikeperch in the Dobczyce Reservoir were different during most of the study period. In late spring/early summer, the studied piscivores were strongly specialized to different prey species. Cormorants consumed mainly roach, the most abundant fish species in the Dobczyce Reservoir. According to the data collected in other studies, roach represent 47.7% of total fish density and 39.4% of total biomass in the limnetic zone (Pociecha & Amirowicz, 2003), and 76–93% of fish density in the littoral zone (Gwiazda & Amirowicz, 2006). An additional advantage of roach as a prey species to cormorants may be that this species aggregates in shoals (De Nie, 1995; Suter, 1997). Roach is the dominant species in the diet of cormorants in many waters (Mellin, 1990; Veldkamp, 1995b; Russell et al., 2003; Wolter & Pawlizki, 2003; Wziatek et al., 2003; Čech et al., 2008) and appears to be preferred for its moderately elongated and thus easy-to-handle body (De Nie, 1995; Dirksen et al., 1995). The body mass of individual roach selected by cormorants in the Dobczyce Reservoir in June–July was relatively large. The middle half of foraged individuals (i.e. those of interquartile total length, 20–26 cm) ranged within 88–210 g (approximated as 4.409×10^{-3} $TL^{3.306}$; A. Amirowicz, unpubl. data).

Pikeperch preferred quite different prey in the first period, both in respect of species and size. Pikeperch mostly consumed juvenile percids, with a predominance of YOY pikeperch in June–July. In comparison to the individual body mass of fish foraged by cormorants, the interquartile body mass of juvenile pikeperch consumed by large conspecifics was very small and ranged within 0.5–1.4 g (4.424×10^{-3} $TL^{3.166}$; A. Amirowicz, unpubl. data). The cannibalistic behaviour of adult pikeperch has been reported many times (more recently by Balık, 1999; Dörner et al., 1999; Frankiewicz et al., 1999; Argillier et al., 2003; Yilmaz & Ablak, 2003; Lappalainen et al., 2006) and this mode of feeding may therefore be recognized as typical for this species, especially in the post-spawning period. Small-sized and abundant prey species occupying an open water habitat offer two advantages to large predatory fish: they cannot escape the much longer predator, and they may easily be encountered at a relatively high rate. Therefore, the YOY pikeperch became important prey of older conspecifics in early summer, despite their low individual biomass.

In mid/late summer both cormorant and pikeperch remained specialized on the prey species consumed in the preceding period, although they also added prey individuals of other size classes into their diets. Cormorants switched towards small fish (juvenile or subadult individuals of 8–12 cm TL for which body mass ranges within 4–16 g in the case of roach) occurring in densities much greater than those of the adult components of their populations. This shift was related to the size pattern of the fish assemblage (Gwiazda & Amirowicz, 2010). Pikeperch widened the size range of their prey by including larger fish of about 20 cm TL and body mass approximating 100 g. This change in pikeperch diet may be explained by a decreased rate of encounter with juvenile percids (Frankiewicz et al., 1999). According to published data, in lacustrine habitats, pikeperch prefer relatively small pelagic prey, e.g. smelt, *Osmerus eperlanus* (Vehanen et al., 1998; Keskinen & Marjomäki, 2004) or vendace, *Coregonus albula* (Kangur et al., 2007) in northern coastal lagoons and glacial lakes, and so it seems probable that the inclusion of other (i.e. larger) fishes into the diet recorded in the Dobczyce Reservoir in summer was forced by insufficient availability of the gradually declining cohorts of juvenile percids. As a result, the prey size distributions in diets of both piscivores became bimodal and similar to each other, i.e. composed of small fish supplemented by occasional relatively large individuals. However, despite the similar importance of particular prey size categories for both cormorant and pikeperch in August–September, their diets retained different species compositions.

In autumn, the composition of diets of both piscivores became similar. They foraged on the same few fish species that are dominant in the fish community of the Dobczyce Reservoir (A. Amirowicz, unpubl. data). Therefore, it may be supposed that the selection of prey species became less targeted towards species that dominated their diets in summer. Prey size distributions continued to be similar in cormorant and pikeperch diets in the third period, and both to some extent resembled the general length distribution pattern of a fish population with several decreasing peaks corresponding to consecutive age classes. Such a prey species and size composition of the diet may be explained by random foraging on available fish. It is possible that the aggregations of wintering fish, which have already started to form in mid-autumn, in the Dobczyce Reservoir (A. Amirowicz, unpubl. data) are attractive for both avian and fish piscivores.

Temperature is another factor that may affect feeding relationships of the two studied species in autumn. In contrast to homoiothermic birds, the rate of metabolic processes in fish depends on water temperature. Pikeperch is regarded as a warm-water species, but its optimal temperature remains only approximately determined and relevant published data are scarce (Wang et al., 2009). The optimal temperature (i.e. a range covering thermal preference, physiological and growth optimum) for this species most probably lies within 24–30°C (Hokanson, 1977; Hilge & Steffens, 1996; Wang et al., 2009). During our study, the measured water temperature in the Dobczyce Reservoir did not exceed 23°C, and the average temperature in the upper 5-m layer of the water column was 21.1, 20.6, and 10.6°C in June–July, August–September, and October–November, respectively (these values are weighted means obtained from the database of measurements sampled from the environmental monitoring continued in the Dobczyce

Reservoir; G. Mazurkiewicz-Boroń, unpublished data). Thus, it may be supposed that the rate of food consumption by pikeperch was relatively high during the first two periods and markedly decreased in the last period. According to the experimental data presented by Molnár & Tölg (1962), the temperature coefficient (Q_{10}) of prey digestion calculated for the range 5–25°C is equal to 3.12. Koed (2001) studied evacuation in pikeperch within a narrower temperature range of 7.8–16.5°C and estimated the Q_{10} value as 4.5. Assuming that feeding rate maintains an average stomach fullness which is permanently reduced by digestion (according to Eggers, 1977; see also Eggers, 1979; Elliott, 1979), the amount of fish consumed by the pikeperch population of the Dobczyce Reservoir in October–November may be estimated at roughly 1/4–1/3 of that foraged in June–July and August–September. Undoubtedly, such a decrease of consumption rate greatly reduced the impact of the pikeperch population on food resources and weakened any feeding interactions with cormorants, despite the significant dietary overlap between these species in the October–November period.

The differences in dietary composition of cormorant and pikeperch recorded in the Dobczyce Reservoir may have resulted from different foraging habits of these piscivores. Cormorants must catch their prey during a short diving cycle lasting 15–71 s (Cramp & Simmons, 1977), with such diving being relatively costly (231.0 kJ h^{-1} in comparison to 23.7 kJ h^{-1} for diving and resting, respectively; Carss, 1997) because of their poor insulation and inefficient foot propulsion (Enstipp et al., 2005). Pikeperch is more limited by the energetic cost of swimming than by the time interval necessary for detection and capture of single prey, and does not bear thermoregulation expense. Differences in the mode of foraging can lead to differences in diet composition in sympatric but phylogenetically distant piscivores (Humphries et al., 1992). Similar differences were also observed between terrestrial carnivores foraging on relatively small prey. Capizzi & Luiselli (1996) investigated feeding relationships between four species of owls and four species of snakes that were sympatric in an agro-forest landscape of central Italy and reported that competition for food seems to be higher between phylogenetically related taxa. However, the phylogenetic distance does not preclude similarity of diet in every case. Goldsworthy et al. (2001) showed a distinct dietary overlap between toothfish and gentoo penguins, *Pygoscelis papua*, around Macquarie Island. Similar results were provided by Van Eerden et al. (1993), who evidenced the predation of both great crested grebe and perch on smelt in IJsselmeer.

The difference between size of prey selected by cormorant and pikeperch in the Dobczyce Reservoir may be adequately explained by the quite different costs of capturing particular prey for these piscivores. In an optimally foraging predator, the predator's behaviour should both maximize gains provided by available prey and reduce foraging expenses. Costs of all components of predation (i.e. prey search, encounter, pursuit, capture, and handling) may be considerably reduced if the prey to predator size ratio is low. In cormorants, a tendency to select small prey has been documented in some studies. This bird is able to catch and swallow fairly large fish (46–47 cm for pike and pikeperch and 65–70 cm for eel; Cramp & Simmons, 1977; Del Hoyo et al., 1992; Keller, 1995; Martyniak et al., 2003); however, it often forages on considerably smaller prey below 15 cm TL (Mellin, 1990; Adámek & Guziur, 1992; Wolter & Pawlizki, 2003). The shift of cormorant towards small fish for prey in autumn, related to fish availability, was documented in the Dobczyce Reservoir (Gwiazda & Amirowicz, 2010). The maximal length of the prey of pikeperch is in general approximated to be about half its own length (Deelder & Willemsen, 1964), which equates to a possible range of 27.5–37.5 cm in our study. Dörner et al. (2007) reported an extreme value of the prey/pikeperch length ratio, at 0.63, in the Bautzen Reservoir, Germany. However, although the largest prey size ratio recorded in the Dobczyce Reservoir was 0.451, it was distinctly smaller (median = 0.102, $Q_1 = 0.083$, $Q_3 = 0.174$) for most of the prey fish collected in this study. Turesson et al. (2002) consider that the selection of small prey by pikeperch maximizes energy intake.

According to our results, it seems probable that both cormorant and pikeperch aimed to select small fishes in the Dobczyce Reservoir and both were constrained to modify their choice, but each of them in different periods and for different reasons. Cormorants must wait until the juvenile cohorts of prey species achieve a threshold biomass to make the single diving cycle profitable (Van Eerden & Voslamber, 1995). For pikeperch, which follow their prey underwater, the minimal prey biomass does not matter but more important is the cruising cost, which is proportional to the prey searching time (i.e. to the cruising distance) in this piscivore. For this reason, a threshold prey encounter rate seems to be a crucial factor in the foraging cost of pikeperch. The continuous decline in abundance of the most preferred small-sized percid juveniles makes it necessary to supplement their ration with larger fishes in the late summer and autumn. The considerably increasing share of large fishes (over 15 cm TL; Fig. 3) in pikeperch diet during the growing season is also clear evidence of their ability to find and capture them, and allows us to reject the possible explanation that selection of small prey may not be the real preference, but rather an effect of size-dependent capture success (Juanes & Conover, 1994).

In conclusion, this study highlights the importance of two components of foraging strategy which, in combination, act to reduce the diet similarity between cormorant and pikeperch foraging within a relatively small feeding area. Both piscivores were seasonally specialized on different prey species, which minimized the dietary overlap, and their different ecological features influenced seasonal differences in the length distributions of selected prey. In general, such differences in selected prey species, and the preferred prey size, probably effectively preclude possible competition and may be important for co-occurrence of two piscivores. In addition, water temperature may periodically modify the relative impact of predatory fish on prey that is shared with a sympatric piscivorous bird. As all these differences result from general biological characteristics specific to birds and fishes, they may also be demonstrated in other cases of piscivorous birds and predatory fishes sharing common food resources.

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References

Adámek, Z. & J. Guziur, 1992. Food composition of black cormorant (*Phalacrocorax carbo* L.) in lowland reservoirs Nové Mlýny (south Moravia, Czechoslovakia). Acta Academiae Agriculturae Technicae Olstenensis 19: 109–120 [in Polish with English summary].

Amirowicz, A., 1998. Consequences of the basin morphology for fish community in a deep-storage submontane reservoir. Acta Hydrobiologica 39(Suppl. 1): 35–56.

Argillier, C., M. Barral & P. Irz, 2003. Growth and diet of the pikeperch *Sander lucioperca* (L.) in two French reservoirs. Archives of Polish Fisheries 11(1): 99–114.

Balık, İ., 1999. The feeding features of the pike-perch (*Stizostedion lucioperca*) population in Lake Beyşehir. Turkish Journal of Zoology 23: 189–194.

Beattie, L. A. & T. D. Nudds, 1989. Differential habitat occupancy by goldeneye ducklings (*Bucephala clangula*) and fish: predator avoidance or competition? Canadian Journal of Zoology 67: 475–482.

Blalock, H. M., 1960. Social Statistics. McGraw-Hill, New York, Toronto, London.

Bur, M. T., M. A. Stapanian, G. Bernhardt & M. W. Turner, 2008. Fall diets of red-breasted Merganser (*Mergus serrator*) and walleye (*Sander vitreus*) in Sandusky Bay and adjacent waters of Western Lake Erie. American Midland Naturalist 159(1): 147–161.

Capizzi, D. & L. Luiselli, 1996. Feeding relationships and competitive interactions between phylogenetically unrelated predators (owls and snakes). Acta Oecologica 17(4): 265–284.

Carss, D. N., 1997. The diet assessment and food intake working group. Supplementi di Ricerche Biologia Selvaggina 26: 197–230.

Čech, M., P. Čech, J. Kubečka, M. Prchalova & V. Draštík, 2008. Size selectivity in summer and winter diets of great cormorant (*Phalacrocorax carbo*): does it reflect season-dependent difference in foraging efficiency? Waterbirds 31(3): 438–447.

Cramp, S. & K. E. L. Simmons (eds), 1977. Handbook of the Birds of Europe, the Middle East and North Africa. Vol. 1: The Birds of Western Palearctic. Oxford University Press, Oxford.

De Nie, H., 1995. Changes in the inland fish populations in Europe in relation to the increase of the Cormorant *Phalacrocorax carbo sinensis*. Ardea 83(1): 115–122.

Deelder. C. L. & J. Willemsen. 1964. Synopsis of biological data on pike-perch *Lucioperca lucioperca* (Linnaeus) 1758. FAO Fisheries Synopsis No. 28: 1–52.

Del Hoyo, J. A., J. A. Elliott & J. Sargatal, 1992. Handbook of the Birds of the World, Vol. 1. Lynx Edicions, Barcelona: 376–429.

Dirksen, S., T. J. Boudewijn, R. Noordhuis & E. C. L. Marteijn, 1995. Cormorants *Phalacrocorax carbo sinensis* in shallow eutrophic freshwater lakes: prey choice and fish consumption in the non-breeding period and effects of large-scale fish removal. Ardea 83(1): 167–184.

Dörner, H., A. Wagner & J. Benndorf, 1999. Predation by piscivorous fish on age-0 fish: spatial and temporal variability in a biomanipulated lake (Bautzen reservoir, Germany). Hydrobiologia 408(409): 39–46.

Dörner, H., S. Hülsmann, F. Hölker, C. Skov & A. Wagner, 2007. Size-dependent predator–prey relationships between pikeperch and their prey fish. Ecology of Freshwater Fish 16: 307–314.

Eadie, J. M. & A. Keast, 1982. Do goldeneye and perch compete for food? Oecologia 55: 225–230.

Eggers, D. M., 1977. Factors in interpreting data obtained by diel sampling of fish stomachs. Journal of the Fisheries Research Board of Canada 34: 290–294.

Eggers, D. M., 1979. Comment on some recent methods for estimating food consumption by fish. Journal of the Fisheries Research Board of Canada 36: 1018–1019.

Elliott, J. M., 1979. Comment on some recent methods for estimating food consumption by fish. Journal of the Fisheries Research Board of Canada 36: 1020.

Engström, H. & L. Jonsson, 2003. Great cormorant *Phalacrocorax carbo sinensis* diet in relation to fish community structure in a freshwater lake. Vogelwelt 124(Suppl.): 187–196.

Enstipp, M. R., D. Grémilet & S. H. Lorentsen, 2005. Energetic costs of diving and thermal status in European shags (*Phalacrocorax aristotelis*). Journal of Experimental Biology 208: 3451–3461.

Eriksson, M. O. G., 1979. Competition between freshwater fish and Goldeneyes *Bucephala clangula* (L.) for common prey. Oecologia 41: 99–107.

Frankiewicz, P., K. Dąbrowski, A. Martyniak & M. Zalewski, 1999. Cannibalism as a regulatory force of pikeperch, *Stizostedion lucioperca* (L.), population dynamics in the lowland Sulejow reservoir (Central Poland). Hydrobiologia 408–409: 47–55.

Godlewska, M. & A. Świerzowski, 2003. Hydroacoustical parameters of fish in reservoirs with contrasting levels of eutrophication. Aquatic Living Resources 16: 167–173.

Godlewska, M., A. Świerzowski, V. Menshutkin & J. Wanzeböck, 2005. Can we precisely estimate fish sizes using acoustics? Hydroacoustics 8: 1–8.

Goldsworthy, S. D., X. He, G. N. Tuck, M. Lewis & R. Williams, 2001. Trophic interactions between the Patagonian toothfish, its fishery, and seals and seabirds around Macquarie Island. Marine Ecology Progress Series 218: 283–302.

Gwiazda, R., 1996. Bird assemblages and the diet of waterfowl at the Dobczyce dam reservoir in the first years of its existence. Folia Zoologica 45(2): 161–169.

Gwiazda, R., 2006. Foraging strategies of fish-eating birds in condition of artificial reservoirs in southern Poland. Studia Naturae 51: 1–112. (in Polish with English summary).

Gwiazda, R. & A. Amirowicz, 2006. Selective foraging of Grey Heron *Ardea cinerea* L., 1758 in relation to density and composition of littoral fish community in a submontane dam reservoir. Waterbirds 29(2): 226–232.

Gwiazda, R. & A. Amirowicz, 2010. Towards the optimal foraging strategy: is seasonal shift in the diet of cormorants *Phalacrocorax carbo* in a dam reservoir the effect of water temperature or size pattern in fish assemblages? Polish Journal of Ecology 58(4): 783–792.

Hilge, V. & W. Steffens, 1996. Aquaculture of fry and fingerling of pikeperch (*Stizostedion lucioperca* L.): a short review. Journal of Applied Ichthyology 12: 167–170.

Hokanson, K. E. F., 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. Journal of the Fisheries Research Board of Canada 34(10): 1524–1550.

Horoszewicz, L., 1960. The value of lower pharyngeal arches as species criteria for defining fish of the Cyprinidae family. Roczniki Nauk Rolniczych 75-B-2: 237–256 [in Polish with English summary].

Humphries, P., G. A. Hyndes & I. C. Potter, 1992. Comparison between the diets of distant taxa (teleost and cormorant) in an Australian estuary. Estuaries 15(3): 327–334.

Jepsen, N., A. Koed & F. Økland, 1999. The movements of pikeperch in a shallow reservoir. Journal of Fish Biology 54(5): 1083–1093.

Juanes, F. & D. O. Conover, 1994. Piscivory and prey size selection in young of-the-year bluefish: predator preference or size-dependent capture success? Marine Ecology Progress Series 114: 59–69.

Kangur, P., A. Kangur & K. Kangur, 2007. Dietary importance of various prey fishes for pikeperch *Sander lucioperca* (L.) in large shallow Lake Võrtsjärv (Estonia). Proceedings of the Estonian Academy of Sciences: Biology, Ecology 56(2): 154–167.

Keller, T., 1995. Food of cormorants *Phalacrocorax carbo sinensis* wintering in Bavaria, southern Germany. Ardea 83: 185–192.

Keskinen, T. & T. J. Marjomäki, 2004. Diet and prey size spectrum of pikeperch in lakes in central Finland. Journal of Fish Biology 65(4): 1147–1153.

Koed, A., 2001. The effects of meal size, body size and temperature on gastric evacuation in pikeperch. Journal of Fish Biology 58(1): 281–290.

Kubečka, J., 1993. Succession of fish communities of Central and East European reservoirs. In Straskraba, M., J. S. Tundisi & A. Duncan (eds), Comparative Reservoir Limnology and Water Quality Management. Kluwer, Dordrecht: 153–168.

Langton, R. W., 1982. Diet overlap between the Atlantic cod *Gadus morhua*, silver hake *Merluccius bilinearis* and fifteen other northwest Atlantic finfish. Fishery Bulletin 80: 745–759.

Lappalainen, J., M. Olin & M. Vinni, 2006. Pikeperch cannibalism: effects of abundance, size and condition. Annales Zoologici Fennici 43: 35–44.

Lindell, L., M. Mellin, P. Musil, J. Przybysz & H. Zimmerman, 1995. Status and population development of breeding cormorants *Phalacrocorax carbo sinensis* of the Central European flyway. Ardea 83(1): 81–92.

Martyniak, A., B. Wziątek, U. Szymańska, P. Hliwa & J. Terlecki, 2003. Diet composition of great cormorants *Phalacrocorax carbo sinenesis* at Kąty Rybackie, NE Poland, as assessed by pellets and regurgitated prey. Vogelwelt 124(Suppl.): 217–225.

Mellin, M., 1990. Preliminary results of the dissection of cormorants shot in the Mazurian Lakeland in spring 1987. Notatki Ornitologiczne 31 (1–4): 53–60 [in Polish with English summary].

Molnár, G. & I. Tölg, 1962. Experiments concerning gastric digestion of pike perch (*Lucioperca lucioperca*). Acta Biologica Hungarica 13(3): 231–239.

Morisita, S., 1959. Measuring of interspecific association and similarity between communities. Memoirs of the Faculty of Science, Kyushu University Series E 3: 65–80.

Mous, P. J., W. Dekker, J. J. De Leeuw, M. R. van Eerden & W. L. T. van Densen, 2003. Interactions in the utilisation of small fish by piscivorous fish and birds, and the fishery in IJsselmeer. In Cowx, J. G. (ed.), Interaction Between Fish and Birds: Implications for Management. Blackwell Science Ltd, Oxford: 84–118.

Pielou, E. C., 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13: 131–144.

Pociecha, A. & A. Amirowicz, 2003. An attempt to determine the share of zooplankton in food consumed by fish in the limnetic zone of a eutrophic dam reservoir. Oceanological and Hydrobiological Studies 32(2): 15–31.

Poulet, N., C. Arzel, S. Messad, S. Lek & C. Argillier, 2005. Diel activity of adult pikeperch *Sander lucioperca* (L.) in a drainage canal in the Mediterranean basin during spring. Hydrobiologia 543: 79–90.

Russell, I. C., A. C. Cook, D. A. Kinsman, M. J. Ives & N. J. Lower, 2003. Stomach content analysis of great cormorants *Phalacrocorax carbo* at some different fishery types in England and Wales. Vogelwelt 124(Suppl.): 255–259.

Starzecka, A., T. Bednarz & A. Amirowicz, 1999. Model of energy flow in the bottom sediments of littoral zone of a dam reservoir with regard to detritivorous roach *Rutilus rutilus* (L.). Polish Journal of Ecology 47: 103–112.

Stempniewicz, L., A. Martyniak, W. Borowski & M. Goc, 2003. Fish stocks, commercial fishing and cormorant predation in the Vistula Lagoon, Poland. In Cowx, J. G. (ed.), Interactions Between Fish and Birds: Implications for Management. Blackwell Science Ltd, Oxford: 51–64.

Suter, W., 1997. Roach rules: shoaling fish are a constant factor in the diet of cormorants *Phalacrocorax carbo* in Switzerland. Ardea 85(1): 9–27.

Turesson, H., A. Persson & C. Brönmark, 2002. Prey size selection in piscivorous pikeperch (*Stizostedion lucioperca*) includes active prey choice. Ecology of Freshwater Fish 11(4): 223–233.

Van Eerden, M. R. & B. Voslamber, 1995. Mass fishing by cormorants *Phalacrocorax carbo sinenesis* at Lake IJsselmeer, The Netherlands: a recent and successful adaptation to a turbid environment. Ardea 83(1): 199–212.

Van Eerden, M. R., T. Piersma & R. Lindeboom, 1993. Competitive food exploitation of smelt *Osmerus eperlanus* by great crested grebe *Podiceps cristatus* and perch *Perca fluviatilis* at Lake IJsselmeer, The Netherlands. Oecologia 93: 463–474.

Van Eerden, M. R., K. Koffijberg & M. Platteeuw, 1995. Riding on the crest of wave: possibilities and limitations for a thriving population of migratory cormorants *Phalacrocorax carbo* in man-dominated wetlands. Ardea 83(1): 1–10.

Vehanen, T., P. Hyvärinen & A. Huusko, 1998. Food consumption and prey orientation of piscivorous brown trout (*Salmo trutta*) and pikeperch (*Stizostedion lucioperca*) in a large regulated lake. Journal of Applied Ichthyology 14(1–2): 15–22.

Veldkamp, R., 1995a. The use of chewing pads for estimating the consumption of cyprinids by cormorants *Phalacrocorax carbo*. Ardea 83(1): 135–138.

Veldkamp, R., 1995b. Diet of cormorants *Phalacrocorax carbo sinensis* at Wanneperveen, The Netherlands, with special reference to bream *Abramis brama*. Ardea 83(1): 143–155.

Wagner, B. M. A., 1997. Influence of fish on the breeding of the red-necked grebe *Podiceps grisegena* (Boddaert, 1783). Hydrobiologia 344: 57–63.

Wagner, B. M. A. & L. A. Hansson, 1998. Food competition and niche separation between fish and the Red-necked Grebe *Podiceps grisegena* (Boddaert, 1783). Hydrobiologia 368: 75–81.

Wang, N., X. Xu & P. Kestemont, 2009. Effect of temperature and feeding frequency on growth performances, feed efficiency and body composition of pikeperch juveniles (*Sander lucioperca*). Aquaculture 289: 70–73.

Winfield, D. K. & I. J. Winfield, 1994. Possible competitive interactions between overwintering tufted duck (*Aythya fuligula* (L.)) and fish populations of Lough Neagh, Northern Ireland: evidence from diet studies. Hydrobiologia 279(280): 377–386.

Winfield, I. J., D. K. Winfield & C. M. Tobin, 1992. Interactions between the roach, *Rutilus rutilus*, and waterfowl populations of Lough Neagh, Northern Ireland. Environmental Biology of Fishes 33: 207–214.

Wolter, C. & R. Pawlizki, 2003. Seasonal and spatial variation in cormorant predation in a lowland floodplain river. In Cowx, I. G. (ed.), Interactions Between Fish and Birds: Implications for Management. Blackwell Science Ltd, Oxford: 178–186.

Wziątek, B., A. Martyniak, U. Szymańska, J. Kozłowski & D. Dostatni, 2003. Composition of the great cormorant *Phalacrocorax carbo sinensis* diet in the Drawa National Park, NW-Poland. Vogelwelt 124(Suppl.): 291–295.

Yilmaz, M. & Ö. Ablak, 2003. The feeding behavior of pikeperch (*Sander lucioperca* (L., 1758)) living in Hirfanlı Dam Lake. Turkish Journal of Veterinary and Animal Sciences 27: 1159–1165.