POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	58	4	783–792	2010

Regular research paper

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TOWARDS THE OPTIMAL FORAGING STRATEGY: IS SEASONAL SHIFT IN THE DIET OF CORMORANTS *PHALACROCORAX CARBO* (L.) IN A DAM RESERVOIR THE EFFECT OF WATER TEMPERATURE OR SIZE PATTERN IN FISH ASSEMBLAGES?

ABSTRACT: According to optimal foraging theory the prey choice strongly affects the benefit-cost ratios. Predators search prey giving the highest benefit and costs of all components of predation (*i.e.* prey search, encounter, pursuit, capture, and handling) may be considerably reduced if the prey is more available. The study on Cormorant diet and the species composition of prey fish assemblages in the Dobczyce Reservoir (area 985 ha, submontane, eutrophic reservoir in Southern Poland) in spring (May-June) and in autumn (Oct-Nov) showed differences in the food composition and the prey size affected by seasonal changes in fish availability. The diet of Cormorant included eleven fish species and the dominant species in the food was roach in spring (72%) and roach and perch in autumn (49% in total). Roach and perch had the highest share in prey assemblages too (56% in spring, and 53% in autumn). Significant preference toward roach in spring was found. The share of roach and perch did not changed seasonally and could not explain the change in the composition of Cormorant diet. The range of the total length (LT) of fish in Cormorant diet was 3.5–35.2 cm. Diet consisted of distinctly smaller fish in autumn. Relative number of small fish was *ca* 3 times greater in this period compared to spring. Weighted mean of fish TL in prey assemblage was 20.0 cm for roach and 12.5 cm for perch in spring, and 11.8 and 8.1 in autumn, respectively. The proportion of average weight of roach ($W = 0.004074\ LT^{3.334}$) to that of perch ($W = 0.005779\ LT^{3.260}$) was greater in spring (4.1:1) than in autumn (2.9:1). Probably it can explain the diet shift in autumn. The switch to smaller but more abundant fish in autumn was not related to temperature but to fish availability which reduced the cost of searching and the prey may be easily found.

KEY WORDS: roach, perch, diet composition, prey size, fish availability, diet shift

1. INTRODUCTION

According to the optimal foraging theory predators search prey giving the highest energetic benefit. It is maximized by food choice (MacArthur and Pianka 1966, Stephens and Krebs 1986). Cormorant *Phalacrocorax carbo* (Linnaeus, 1758) is a fish-eating bird that pursuits and captures its prey underwater (Cramp and Simmons 1977). Seasonal changes in a food composition was studied in different areas and periods (Dirksen *et al.* 1995, Seiche 2003, Wziątek *et al.* 2003,

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The paper was presented on the XXI Congress of Polish Hydrobiologists, 9–12 September 2009, Lublin, Poland.

Lehikoinen 2005, Lekuona 2007, Čeh *et al.* 2008, Liordos and Goutner 2008). Therefore, only a general supposition may be made that Cormorants forage on the species dominant in the fish community (Martyniak *et al.* 2003, Russell *et al.* 2003, Stempniewicz *et al.* 2003).

In a situation when foraged prey is not abundant, a predator shifts toward less profitable, but available food (Schoener 1971, Pyke 1979).

Van Eerden and Voslamber (1995) and Čeh *et al.* (2008) suggested that temperature is the key factor of the Cormorant diet shift, because of the temperature-induced changes in muscle efficiency of poikilothermic fish. According to these authors, in higher temperature Cormorants reduce the increase of hunting cost by shifting towards smaller prey, *i.e.* selecting fish which maximum speed is lower, what results from the relation between fish body length and its possible velocity. However, as the body mass of a fish depends on the third power of its length, such prey choice strongly affects the benefit-cost ratio. Therefore, an alternative strategy of maximization the energetic benefit which relies on prey availability may be considered. In other words, if a prey category is more costly but far more available than another, it may allow predator to profit, despite the elevated overall cost.

The aim of this study was to test above supposition, by comparing the fish size distribution in Cormorant diet and in fish assemblage in two periods similar in composition of prey fish assemblage. The results may help to better understand the factors determining differences in Cormorant diet within their occurrence range.

2. STUDY AREA

The study was carried out on the Dobczyce Reservoir (49°52´N, 20°02´E, altitude 270 m) located on the Raba river in southern Poland about 30 km south from Cracow (Fig. 1). It is a submontane, eutrophic reservoir with an area of 985 ha, volume of 108 GL, shoreline of *ca* 42 km, mean depth of 11.0 m (max. *ca* 27 m), and mean water residence time 0.34 yr (Amirowicz 1998). In general, the littoral zone is narrow because of relatively steep slopes of the inundated river valley. The beds of aquatic macrophytes are restricted to the shallow bay in a long flat lateral valley of the Wolnica stream, and to few other small areas (more abundant are *Phragmites australis* (Cav.) Trin. ex Steud., *Polygonum amphibium* L. and several species of the genera *Typha*, *Myriophyllum*, *Potamogeton* and *Batrachium*). The approximate value of annual mean air temperature is in range of 7.5–8.0°C (the extreme monthly averages are about −4–−3°C in January and 17–18°C in July). Usually the reservoir is ice covered in January and February. The main function of the Dobczyce Reservoir is the storage of water for municipal purposes.

The fish community consists of 19 species (Amirowicz 2000). The dominants are five cyprinid and percid species, roach *Rutilus rutilus* (L.), bream *Abramis brama* (L.), bleak *Alburnus alburnus* (L.), perch *Perca fluviatilis* L. and pikeperch *Sander lucioperca* L. Some lower ranks hold white bream *Blicca bjoerkna* (L.), rudd *Scardinius erythrophthalmus* (L.), and chub *Leuciscus cephalus* (L.). Remaining eleven species can be regarded as relatively rare. The fish biomass in littoral zone estimated by shore seining reached 233 kg ha^{-1} (only individuals > 20 cm TL; Starzecka *et al.* 1999). The relative fish density in limnetic zone estimated in acoustic surveys conducted in 2000–2002 was 3390–5625 ind. ha^{-1} (individuals > 2.8 cm TL; Godlewska and 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}. In the avifauna dominated Great Crested Grebe, *Podiceps cristatus* (L.), Mallard, *Anas platyrhynchos* L., and Black headed Gull, *Larus ridibundus* L. (Gwiazda 1996). In the late 1990s the increasing in number Grey Heron *Ardea cinerea* L. and Cormorant were dominant species as well (Gwiazda 2003). Usually number of Cormorants is lower than 100 ind. and peak numbers are recorded in autumn (max. abundance, > 600 ind. was noted).

3. MATERIAL AND METHODS

The diet of Cormorant was studied by examination of pellets. Pellets were collected on

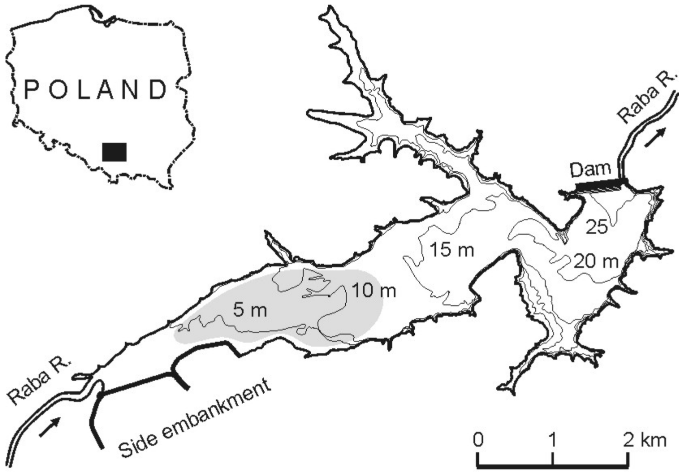

Fig. 1. The main foraging area (shaded) of Cormorant *Phalacrocorax carbo* (L.) in the Dobczyce Reservoir.

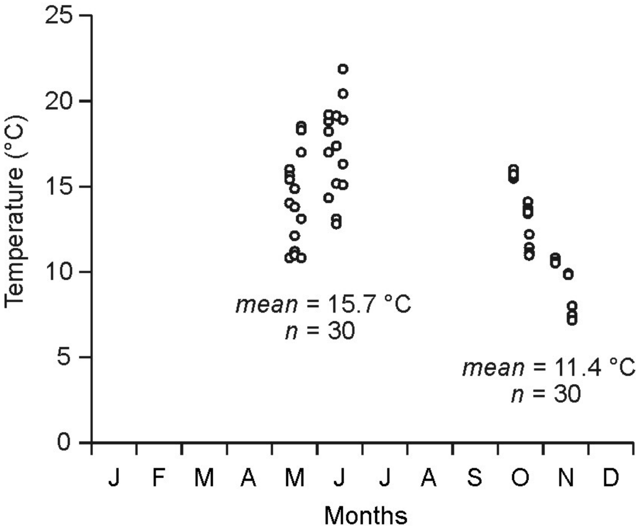

Fig. 2. Temperature of water in spring (May-June) and autumn (October-November) in the Dobczyce Reservoir during the period of study (2002, 2004, and 2005; G. Mazurkiewicz-Boroń, unpubl.).

the roost in spring (May-June) and in autumn (October-November) in 2002, 2004 and 2005 (N = 90). Fish remains were identified based on pharyngeal bones and chewing pads (cyprinids), otoliths (percids), and jaws (pike, *Esox lucius* L., pikeperch). The number of individuals of a species represented in a pellet was approximated by the highest total of any of the identifiable parts present, taking right and left parts separately. They were measured to calculate the prey length with using published regression formulae (otoliths – Dirksen *et al.* 1995, pharyngeal bones – Horoszewicz 1960, chewing pads – Veldkamp 1995a). The composition of diet was assessed by summing weighted averages of numbers of particular prey fish species.

The composition of assemblage of potential prey was assessed on the basis of gill net catches. Fish were caught by the gill net set composed of four panels (mesh size 10, 20, 30, and 40 mm which select individuals within the whole length range of possible prey of Cormorants) in the littoral zone in June and October. Nets were exposed overnight at sites chosen within the Cormorant feeding areas. Content of each net panel was stored separately. The exposition of the running meter of net panel was regarded as the single unit of effort, and the respective number of fishes caught as the catch per unit of effort (CPUE). Species composition of fish community was approximated by the sum of CPUEs of four panels of the gill net set. Collected fishes were measured and weighed to allow calculate length-weight relationships.

The average temperature of water in periods of collecting the pellets was provided by G. Mazurkiewicz-Boroń (unpublished data; a part of long-term monitoring data on selected habitat factors in the Dobczyce Reservoir collected since 1986). The data set composed of the results of temperature measurements in the water column from the surface down to the depth of 10 m, at 2.5 m depth intervals, done on twelve sampling dates (*i.e.* two in each season and year of study) was used. In general, water temperature was lower by about 4°C in autumn (Fig. 2) and this difference was significant (the *t*-test, $P < 0.001$).

The significance of differences in proportion of selected fish species in Cormorant diet between seasons were determined by Chi-square test (Yates' correction was used) (Zar 1996), while the Mann-Whitney test was used to estimate the significance of differences between the prey lengths in Cormorant diet between seasons (Blalock 1960).

4. RESULTS

Roach, perch, white bream, *Abramis brama* (L.), and ruff, *Gymnocephalus cernuus* (L.), were the most abundant species in fish assemblages, which constituted 79% of the whole fish number in spring (N = 222), and 92% in autumn (N = 417). The range of fish total length was 5.9–51.2 cm in fish assemblages. The species composition remained relatively stable (Fig. 3), while the fish abundance and size distribution pattern changed considerably. Total fish abundance recorded in autumn was three times greater than in spring (Table 1). This overall increase may be exclusively attributed to the greatly increased number of fish caught in gill net panel of 10-mm mesh, *i.e.* to the YOY (young-of-the-year) fishes. The CPUEs of panels with greater mesh may be considered as unchanged. Thus, within the foraging area the number of small-sized fish considerably changes seasonally and strongly affects both the density and size pattern of Cormorant prey. Weighted mean of fish total length in assemblage was 20.0 cm for roach and 12.5 cm for perch in spring and 11.8 and 8.1 in autumn, respectively. The proportion of average weight of roach ($W = 0.004074\ LT^{3.334}$) to that of perch

Table 1. Approximated fish abundance and species composition of the prey fish assemblage within Cormorant foraging area in the Dobczyce Reservoir in 2005 (CPUE – catch per unit of effort; for calculation procedure see the chapter "Material and methods").

Species	Number of fishes in gill net panels				CPUE	Relative abundance (%)
Mesh size (mm)	10	20	30	40		
Panel length (m)	9.4	19.8	20.3	36.0		
Spring						
Blicca bjoerkna (L.)		7	7	15	1.12	9
Gymnocephalus cernuus (L.)	17				1.81	14
Perca fluviatilis L.	24	10	3	3	3.29	26
Rutilus rutilus (L.)	5	32	34	4	3.93	30
Others		32	12	17	2.68	21
CPUE	4.89	4.09	2.76	1.08	12.83	100
Autumn						
Blicca bjoerkna (L.)	107			4	11.49	32
Gymnocephalus cernuus (L.)	26				2.77	8
Perca fluviatilis L.	81	3		4	8.88	24
Rutilus rutilus (L.)	77	21	8	22	10.26	28
Others	6	17	19	22	3.04	8
CPUE	31.60	2.07	1.33	1.44	36.44	100

Other species: *Abramis brama* (L.), *Alburnus alburnus* (L.), *Aspius aspius* (L.), *Esox lucius* L., *Sander lucioperca* (L.), *Scardinius erythrophthalmus* (L.), roach × bream hybrids

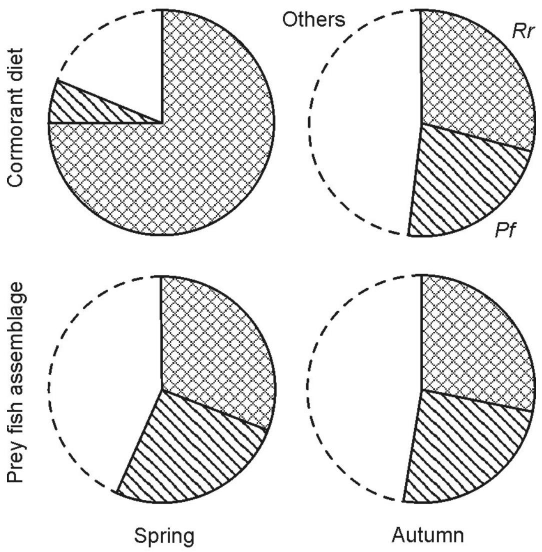

Fig. 3. The share of dominant species in the diet of Cormorant *Phalacrocorax carbo* (L.) and in prey fish assemblage in the Dobczyce Reservoir: *Pf* – perch, *Rr* – roach.

Table 2. The composition of Cormorant diet in the Dobczyce Reservoir.

Species	Weighted mean	Relative share (%)
Spring		
Blicca bjoerkna (L.)	1.2	4
Gymnocephalus cernuus (L.)	0.8	3
Perca fluviatilis L.	1.8	7
Rutilus rutilus (L.)	19.3	72
Others	3.8	14
Total	26.9	100
Autumn		
Blicca bjoerkna (L.)	0.5	1
Gymnocephalus cernuus (L.)	11.2	13
Perca fluviatilis L.	17.5	21
Rutilus rutilus (L.)	23.5	28
Others	31.1	37
Total	83.8	100

Other species: *Abramis brama* (L.), *Alburnus alburnus* (L.), *Carassius* sp., *Cyprinus carpio* L., *Esox lucius* L., *Leuciscus cephalus* (L.), *Sander lucioperca* (L.)

($W = 0.005779\ LT^{3.260}$) was greater in spring (4.1:1) than in autumn (2.9:1).

The majority of Cormorant diet consisted of the same four fish species dominant in the prey assemblage (Table 2) with the highest proportion of roach (72%, N = 79) in spring and roach and perch (28% and 21%, N = 222, respectively) in autumn (Fig. 3). The range of the total length (TL) of fish in Cormorant diet was 3.5–35.2 cm. Median of the length of fish foraged by Cormorants was 21.6 (Q= 18.5 cm, Q= 25.3 cm, N = 62) in spring and 10.8 cm (Q= 7.2 cm, Q= 20.3 cm, N = 201) in autumn. Size of fish in a diet of Cormorant was distinctly greater in spring compared to autumn in all studied years (Z = 6.695, df = 108, $P < 0.001$ in 2002; Z = 3.638, df = 102, $P < 0.001$ in 2004; Z = 2.708, df = 52, $P < 0.01$ in 2005) (Fig. 4).

The comparison of the Cormorant diet compositions showed differences between seasons in proportion of roach ($X^2 = 13.33$, df = 1, $P = 0.0003$). The proportion of fish species in the diet in comparison to fish assemblage showed the dominance toward roach ($X^2 = 4.13$, df = 1, $P = 0.04$) in spring.

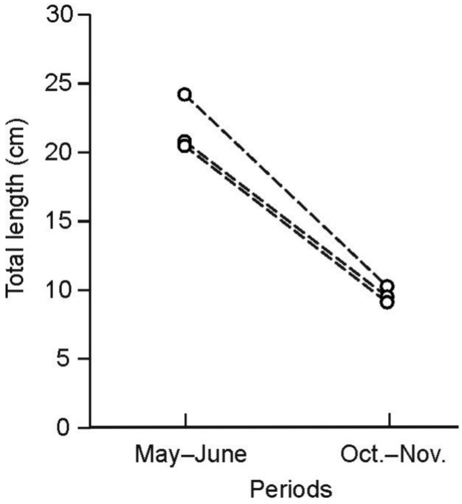

Fig. 4. Median fish length in the diet of Cormorant *Phalacrocorax carbo* (L.) in the Dobczyce Reservoir in spring and autumn in three (2002, 2004, 2005) years of the study.

Such differences were not found for roach in autumn ($X^2 = 0.02$, df = 1, $P = 0.89$) and for perch in both periods ($X^2 = 0.80$, df = 1, $P = 0.37$; $X^2 = 0.04$, df = 1, $P = 0.85$).

5. DISCUSSION

Cormorants foraged mostly on roach in spring (May-June) and on roach and perch in autumn (October-November) in the Dobczyce Reservoir. Results of other studies show another tendency. In the study of Wziątek *et al.* (2003) the proportion of roach increased and perch decreased from May to August in the Ostrowieckie Lake in the Drawa National Park (N-W Poland) and Čeh *et al.* (2008) shows the contribution of roach and chub in the diet of Cormorants in two reservoirs in Czech Republic increased from summer to winter. According to the data collected in a previous study roach amounts to 76–93% of fish density in the littoral zone of the Dobczyce Reservoir (Gwiazda and Amirowicz 2006). Roach and perch are fish species aggregating in shoals and were dominant in Cormorant diets in many lakes (Mellin 1990, Veldkamp 1995*b*, Mellin and Mirowska-Ibron 1997, Wziątek *et al.* 2003, Gmitrzuk 2004, Čeh *et al.* 2008). Greater share of roach and perch in the diet of Cormorant in comparison to the composition of fish assemblage in the Dobczyce Reservoir showed an importance of these species, probably because Cormorant prefers more elongated fish which are easier to handle (De Nie 1995, Čeh *et al.* 2008).

The most important factor that determines a predator's food choice is relative prey availability (Hartman and Margraf 1992). Cormorant can be considered a generalist because it takes fish of variety of species and sizes classes and exploits the most abundant stocks (Keller 1995, Engström and Jonsson 2003). The duration of Cormorant diving cycle is limited and therefore it must caught a prey in short time. Diving is also very costly in this species (Carss 1997) because of their poor insulation and less-efficient foot propulsion (Enstipp *et al.* 2005). Therefore, the good prey is the prey possible to gain relatively quickly. Cormorants wintering in Greenland in very harsh habitat conditions (water temperature about −1°C) take their daily food ration in 9 minutes on average. Such foraging efficiency depends upon dense, highly predictable prey stocks allowing birds to gain sufficient energy during extremely short time (Gremillet *et al.* 2001). Temporal changes of a Cormorant diet in two Greek colonies can be attributed to changes in prey availability and abundance and confirm bird's opportunistic behavior (Liordos and Goutner 2008). However studies in the Lake Ymsen (Sweden) indicated that Cormorants did not take fish in proportion to their occurrence in the fish assemblage (Engström and Jonsson 2003) similar to our results. But in this shallow lake proportion of roach and perch was lower in the Cormorant diet than in the fish assemblage in contrast to higher proportion of ruffe which is slower swimmer.

Availability of small fish in the Dobczyce Reservoir varied during the growing season. Cormorants foraged on smaller fish in the Dobczyce Reservoir in October-November in comparison to May-June period. Čeh *et al.* (2008) found that average total length and weight of fish taken by Cormorant significantly increased with decreasing water temperature at two reservoirs in Czech Republic. Van Eerden and Voslamber (1995) reported reverse switch in prey size in IJsselmeer Lake late May with increasing temperature. These changes in the length of selected prey were caused by differences in temperature, because in higher water temperature swimming speed of fish reach the higher value, so Cormorant switches to smaller prey which swim slower and could be caught at lower costs. The swimming speed of Cormorant does not depend on water temperature but water temperature is an important factor for swimming costs (Grémillet and Wilson 1999). Energetically optimal swimming speed for social foraging Cormorants in IJseelmeer Lake (The Netherlands) was 0.6 m s^{-1} (Van Eerden and Voslamber 1995). This is maximal swimming speed of a fish 5 cm long in temperature 20°C. Maximal speed of the fish 20 cm long is four times greater (2.4 m s^{-1}) in the same temperature (Van Eerden and Voslamber 1995) while the body weight of such roach is about two orders of magnitude greater than that of a 5 cm individual (*i.e.* 90 g and 1 g, respectively).

The switch in Cormorant diet towards small fish in the Dobczyce Reservoir in autumn was not related to water temperature as in above examples (because the temperature in autumn was lower than in spring) but to fish availability. The most probable reason is that in situation when density of small fish is several times greater than that of the large ones, more profitable may be foraging on small fish. Foraging on more numerous cohorts of younger, mainly YOY fish reduce costs of searching and catching prey because small and abundant prey escape less successfully and may be easily found. As the result, the diet become composed of small fish supplemented with occasionally taken relatively large individuals. Such shift toward smaller individuals of roach in Cormorant diet in two lakes in The Netherlands during the growing season was reported (Dirksen *et al.* 1995).

The proportion of roach and perch in the Dobczyce reservoir did not changed seasonally and could not explain the change in Cormorant diet. However, the fish length distribution in assemblages differed between seasons. The greater proportion of average weight of roach to perch in spring than in autumn probably can explain the greater share of roach in spring and shift toward the most numerous fish species (*i.e.* toward a more stochastic sampling in fact) in autumn. Our results suggest that Cormorants chose prey in answer to the changed resource availability. Therefore, we conclude that: (1) the more cost-effective has been foraging on greater fish if the relative size differences between available fish were small, (2) the more cost-effective has been foraging on smaller fish if the smaller fish were much more abundant, (3) the fish size distribution in a fish assemblage was the leading/prevailing factor in prey choice despite the differences in costs of capture of a small and large fish.

ACKNOWLEGEMENTS: The authors thank Dr Grażyna Mazurkiewicz-Boroń, Inst. Nature Conservation PAS, Cracow, who kindly provided the monitoring data collected in the Dobczyce Reservoir.

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Received after revision March 2010