

Differences in the diet of breeding Cormorants *Phalacrocorax carbo sinensis* in an inland colony: the effect of years, breeding stages and locations within the colony

Simone Buttu^{1*}, Giulia Atzori¹, Francesco Palmas¹, Robert Gwiazda²

¹Department of Life and Environment Sciences – Section of Animal Biology and Ecology, University of Cagliari, Via T. Fiorelli, 1-09126 Cagliari, Italy, e-mail: simone.buttu@hotmail.it (*corresponding author)

²Institute of Nature Conservation – Polish Academy of Sciences, Mickiewicza 33, 31-120 Kraków, Poland

Abstract: A study of the diet of the Great Cormorant *Phalacrocorax carbo sinensis* (fish species and size) in (1) different seasons (years), (2) breeding stages (incubation and chick rearing), and (3) breeding areas (center and edge) in the colony in the Dzierżno-Duże Reservoir (southern Poland) was carried out. Overall, 147 pellets of the Great Cormorant were analysed. The low values of the indexes of Levin (B_i) and Shannon (H) showed a limited trophic spectrum in the diet of the Great Cormorant. Roach (*Rutilus rutilus*) with a percentage index of relative importance (%IRI) of 62.89, perch (*Perca fluviatilis*) (%IRI = 22.63) and carp (*Cyprinus carpio*) (%IRI = 10.43), were the most common prey. Evident changes in the diet between 2003 and 2014, with less roach and more perch and ruffe in 2014 were found. They could be probably related to changes in the fish community. Differences in the food of cormorants between breeding stages reflected dietary requirements of the chicks. During the breeding season younger chicks require feeding with smaller fish than older chicks. The proportion of fish species found in the cormorant diet differed between the edge and the centre of the colony. We concluded that the impact of Great Cormorants on native fish assemblages may be dependent on the location within the colony, development state of the chicks and season, not just fish availability.

Key words: Phalacrocorax carbo sinensis, pellet analysis, food composition, fish size, daily food intake.

Introduction

The Great Cormorant, *Phalacrocorax carbo sinensis* (Blumenbach 1798), is an abundant piscivorous top predator that forages on a wide range of fish species (Johnsgard 1993; Lindell 1997; Carss 2003). This species may be considered an opportunistic predator (Leopold et al. 1998) that forages in freshwater habitats (Bearhop et al. 1999), estuaries (Vetemaa et al. 2010) and coastal marine areas (Grémillet et al. 2004). The Great Cormorant nests in the northern areas of the Western Palearctic, and performs short migrations to reach the wintering areas.

The species had become nearly extinct due to persecution in the 19th and the first half of the 20th century (Van Eerden and Gregersen 1995). Following its near extinction, protection measures were established in the northern regions of Europe (EEC 1979; EC 1997). As a consequence, cormorant numbers and the species range of distribution have expanded greatly in recent

years (Van Eerden and Gregersen 1995; Lindell et al. 1995). This is the case in the Silesia region in Poland where the Great Cormorant established a breeding colony in early 1990s (Profus et al. 2002).

Diet studies are important to understand the different food composition in seasonal changes in different areas and periods (Čech et al. 2008; Liordos and Goutner 2008). Cormorant diet composition has been attributed to changed selectivity of fish prey (Keller 1995; Lehikoinen 2005; Čech et al. 2008; Gwiazda and Amirowicz 2010) and/or to changed fish behaviour and movements (Keller 1995; Gwiazda and Amirowicz 2010).

The most important factor of a predator's food choice is relative prey availability (Hartman and Margraf 1992). Generally, cormorants forage on the most numerous species in the fish community and their diet reflects fish availability (Engström and Jonsson 2003; Martyniak et al. 2003; Stempniewicz et al. 2003; Gwiazda and Amirowicz 2010). The number of fish depends on food con-

ditions and reproduction success that can change considerably between seasons. In this situation cormorants' diet can change in the same water bodies (Dirksen et al. 1995; Engström and Jonsson 2003; Stempniewicz et al. 2003; Mous et al. 2003) and the species is able to cover great distances in order to exploit fishing areas far from the reproduction sites (Cramp and Simmons 1977).

The prev of cormorants can also vary during the breeding season (Hobson et al. 1989). Chicks of different age require different fish (size and digestibility) (Platteeuw et al. 1995). The demographic pattern of the winter distribution of the cormorant shows that adult males stay closest to the breeding grounds whereas juvenile immature females migrate furthest to the south (Van Eerden and Munsterman 1995). Cormorants wintering <300 km from the colony arrived on average 2–3 weeks in advance of those wintering >300 km from the colony. Mean fledgling production per individual (3-4 chicks per nest) did not decrease with increasing distance to the wintering area (Wojczulanis-Jakubas et al. 2013). However, lifetime reproductive success of males wintering 301-900 km from the colony is lower (Bregnballe et al. 2006). The birds of better condition can arrive at the colony site earlier than birds of lower condition, and occupy a habitat in the central part of colony. Birds that arrive later in the season settle outside the central part of the colony.

The aim of this study was to determine differences in fish species and size in the diet of the Great Cormorant between: (i) different seasons (years), (ii) breeding stages (incubation and chick rearing), and (iii) breeding areas (centre vs edge) of the colony.

Study area

The study was carried out on the Dzierżno-Duże Reservoir (50°22'N, 18°34'E) (Fig. 1) located on the left bank of the Gliwice channel near Gliwice (Silesia region) in southern Poland. The reservoir is a sand mine excavation, overflowed by the River Kłodnica in 1964. The waters of the Kłodnica were polluted. The area of the reservoir is 615 ha, mean length 5.8 km, mean width – 1.0 km, shoreline c. 16 km, mean depth 15.0 m (max. c. 20 m). In general, the littoral zone is narrow because of the relatively steep slopes of the inundated valley. The main functions of the Dzierżno-Duże Reservoir are flood control, improved conditions for water transport, and water self-purification of the River Kłodnica (Rzetała et al. 2013).

The following species were recorded in the fish community: carp *Cyprinus carpio*, crucian carp *Carassius carassius*, tench *Tinca tinca*, roach *Rutilus rutilus*, bream *Abramis brama*, rudd *Scardinius erythrophthalmus*, bighead carp *Hypophthalmichthys nobilis*, three-spined

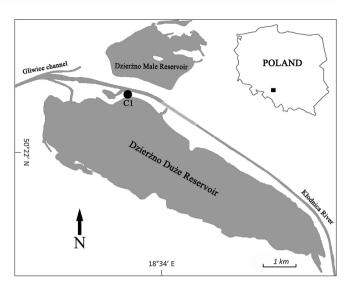


Fig. 1. Map of the study area

stickleback *Gasterosteus aculeatus*, nine-spined stickleback *Pungitius pungitius*, sunbleak *Leucaspius delineatus*, perch *Perca fluviatilis*, ruffe *Gymnocephalus cernuus*, pikeperch *Sander lucioperca*, pike *Esox lucius* and catfish *Silurus glanis* (Kostecki 2000). Roach, carp, crucian carp and perch were the dominant species. In the same area water birds comprised ninety three species (Szlama and Profus 2008). The number of species and flock size of most bird species is lower than in some reservoirs in Poland but some of them were numerous during migration. The maximum number of Mallard *Anas platyrhynchos* was 9873 ind., Black-headed Gull *Chroicocephalus ridibundus* – 7080 ind., Coot *Fulica atra* – 5265 ind. Tufted Duck *Aythya fuligula* – 3900 ind and Smew *Mergus albellus* –0 3000 ind. (Szlama and Profus 2008).

The first breeding colony of the Great Cormorant was established in Dzierżno-Duże Reservoir in 1994. Twenty three nests of the Great Cormorant were counted at this site in 2000 and 106 in 2001 (Profus et al. 2002), and the greatest flocks were recorded from July to November. The highest number of cormorants within the colony (2000 individuals) was recorded in October 2007 (Szlama and Profus 2008).

Methods

The diet of the cormorant was studied by examination of pellets in the breeding colony. A total of 147 fresh pellets were collected on 10 May 2003 (n = 46), 15 April 2014 (n = 44) and 6 June 2014 (n = 57). In order to compare the two breeding seasons in the different years (2003 vs 2014) we matched the data of April and June in one data set. In 2014 the pellets were also sampled in two parts of the colony: the Centre (located in the centre of the breeding colony) and the Edge (about 10 metres from the shore).

Fish remains were identified based on pharyngeal bones and chewing pads (cyprinids), otoliths (percids), and jaws (pike, pikeperch). They were measured to calculate the total length and body mass of each fish using established relationships (otoliths – Dirksen et al. 1995, pharyngeal bones – Horoszewicz 1960, chewing pads – Veldkamp 1995). If the fish length (body length) was estimated from dimensions of pharyngeal bones the estimate was increased by 15% to approximate the total length. 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. The diet composition was assessed by summing weighted averages of numbers of particular prey fish species.

Data collected were analysed both by numerical (Lagardère 1975) and by ponderal analysis (Lauzanne 1982). Percent frequency of occurrence (%FO), percent number (%N), percent weight (%W) and the vacuity coefficient (%Cv) were calculated in order to describe the diet. According to the %N values, prey items were grouped into three categories (%N > 50 dominant prey; 10 < N < 50 secondary prey; %N < 10 accidental prey) (N0 a 1992).

The quantitative importance of each prey group in the diet was also evaluated through the index of relative importance (*IRI*) (Carrassòn et al. 1997):

$$IRI = (\%W + \%N) \cdot \%FO$$

where: %W is the average percent weight, %N is the average percent number and %FO is the percent Frequency of Occurrence.

The percentage *IRI* value of each prey with respect to the total value (Cortés 1997), was estimated using the formula:

$$\%IRI = 100 \cdot \left(\frac{IRI_{ij}}{\Sigma_i IRI_{ij}}\right),$$

where: IRI_{ij} is the absolute IRI value of the prey j in the diet of the species i.

The breadth of the trophic niche was determined by the use of the indexes of Levins (B_i) (Levins 1968):

$$B_i = \left(\frac{1}{n-1}\right) \cdot \left(\frac{1}{\sum_j p_{ij}^2 - 1}\right)$$

where: B_i is the Levins measure of niche breadth and p_{ij} is the proportion of the prey j in the diet of the species i, and Shannon-Weaver (H') (Shannon and Weaver 1949):

$$H' = \sum_{i=1}^{2} p_{ij} \cdot log_{e} \cdot p_{ij}$$

The significance of differences in the proportion of selected fish species in cormorant diet in the two years, breeding stages and parts of the colony were determined by the 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 and parts of the colony (Sokal and Rohlf 1987).

Results

Species composition and fish length in two years

1,413 items were found altogether, 1,363 of which consisted of fish remains. Twelve species were identified in pellets. Overall, Cyprinidae (93.3% of all prey, n = 742) was the most abundant family in the diet, whereas only 6.7% of elements belonged to the Percidae family (Table 1).

Table 1. Numbers (*n*), frequency of occurrence (%*FO*), Percent number (%*N*), Percent weight (%*W*) and Percent Index of Relative Importance (%*IRI*) of prey found in the pellets of the Great Cormorant breeding in the Dzierżno-Duże Reservoir in 2003 and in 2014

Family	Species	2003					2014					
		n	%FO	%N	%W	%IRI	n	%FO	%N	%W	%IRI	
Cyprinidae	Rutilus rutilus	116	86.96	60.1	60.1	83.2	207	64.26	37.88	44.71	52.22	
	Cyprinus carpio	7	19.57	3.63	3.63	1.13	62	34.05	11.05	17.79	13.03	
	Blicca bjoerkna	3	6.52	1.55	1.55	0.16	1	1.89	0.34	3.97	0.09	
	Carassius carassius	2	4.35	1.04	1.04	0.07	2	3.77	0.68	0.87	0.07	
	Chondrostoma nasus	5	10.87	2.59	2.59	0.45	_	_	_	_	_	
	Leuciscus cephalus	1	2.17	0.52	0.52	0.02	-	_	_	_	_	
	Leuciscus leuciscus	15	17.39	7.77	7.77	2.15	_	_	_	_	_	
	Scardinius erythrophthalmus	_	_	_	_	_	1	1.89	0.37	0.46	0.02	
	Abramis brama	_	-	-	-	_	1	1.89	0.37	0.01	0.01	
	Leuciscus idus	_	_	_	_	_	1	1.89	0.54	0.73	0.03	
Percidae	Perca fluviatilis	33	39.13	17.1	17.1	10.65	215	54.58	39.27	18.48	30.65	
	Gymnocephalus cernuus	11	23.91	5.7	5.7	2.17	59	30.17	10.01	2.65	3.97	

The most important prey recorded in 2003 and 2014 was the roach *Rutilus rutilus* (%N = 60.10; %IRI = 83.20; (%N = 37.88; %IRI = 52.22, respectively), while *Perca fluviatilis* (%N = 17.10; %IRI = 10.65; (%N = 39.27; %IRI = 30.65, respectively) was the second most important prey item (i.e. secondary prey) (Table 1). The other fish species were less represented in the diet of cormorants. The average number of fish collected in one pellet was 4.2 (SD ± 3.2 , n = 193, range: 1–11) in 2003 and 6.2 (SD ± 4.1 , n = 553, range: 1–32) in 2014. Significant differences in the proportion of fish species in the cormorant diet between 2003 and 2014 were found ($\chi 2 = 84.20$, df = 11, p = 0.0001).

Among the most important prey in the feeding habits of the cormorant diet, the average total length (TL) of roach was 15.2 cm (SD ± 3.3 , n=116) in 2003 and 14.1 cm (SD ± 4.1 , n=207) in 2014. This species ranged in size from 4.7 cm to 30.5 cm. Average total length of perch was 12.9 cm (SD ± 4.2 , n=33) in 2003 and 11.9 cm (SD ± 3.4 , n=215) in 2014. The range of the total length of this species was between 5.4 and 21.5 cm. The differences between fish length in the cormorant's diet in the two years were statistically significant (Mann-Whitney U test, U = 0.028, p <0.05). The biggest prey ingested by Great Cormorants was represented by a roach with a total length of 32.9 cm.

In terms of biomass (g) of fish consumed, roach (*R. rutilus*) represented 60.1% and 44.7% of total fish biomass in 2003 in 2014 respectively, while perch (*P. fluviatilis*) represented 17.1% (2003) and 18.5% (2014) (Table 1).

Species composition and fish length in two breeding stages

On the whole, 553 individuals, belonging to nine species, were identified. Perch and Ruffe were the most abundant prey within the Percidae family. There was no dominant prey item in the diet (abundance index (%N) was lower than 50% for all prey items). Indeed, Perch (%N = 43.05; %IRI = 37.75; %N = 35.49; %IRI = 23.55,

respectively) and Roach (%N = 36.51; %IRI = 53.43; %N = 39.25; %IRI = 51.02, respectively) were considered as secondary prey (Table 2). The other fish species have been identified as accidental prey (%N < 10). Analysis of the pellets showed that the average number of fish found in one pellet was 6.6 (SD ± 5.1 , n = 169, range: 1–25) in April and 5.8 (SD ± 4.2 , n = 174, range: 1–34) in June 2014. Significant differences were found in the consumption of fish preyed on in the cormorant diet in April and June ($\chi 2 = 20.67$, df = 8, p = 0.008).

The feeding habits showed a different range in total length (TL) among the most abundant prey. Average length of roach and perch was 14.1 cm (SD ± 5.3 , n=129) and 11.1 cm (SD ± 3.2 , n=206) in April, respectively. These values was 12.9 cm (SD ± 4.3 n=123) and 9.5 cm (SD ± 2.1 , n=208) for both species in June. Perch showed a size ranging between 4.7–21.5 cm and roach from 3.7 to 32.9 cm. Significant differences in fish length preyed on in the two breeding stages were found (Mann-Whitney U test, U = 0.009, p <0.05).

In both breeding stages the total biomass of prey was mostly represented by *R. rutilus* (45.31% and 44.10% for April and June respectively) and *P. fluviatilis* (15.69% and 20.28% for April and June respectively) (Table 2).

Species composition and fish length in two parts of the colony

Analysing 421 items, it was possible to identify a total of 293 individuals, belonging to nine species. Among these species in both locations roach R. rutilus represented the most important prey (%N = 29.61; %IRI = 48.72; %N = 54.39; %IRI = 66.22, respectively), whileperch P. fluviatilis and common carp C. carpio were considered as secondary prey (Table 3). Conversely, ruffe G. cernuus was found exclusively in the samples collected from the edge of the colony (%N = 12.29). The other fish species were considered as accidental prey (%N < 10) (Table 3).

The average number of fish per pellet was 6.3 (SD ± 4.2 , n = 179) at the edge and 4.9 (SD ± 5.3 , n = 114) in the centre of the colony. Significant differences between

Table 2. Diet of *P. carbo sinensis* in the Dzierżno-Duże Reservoir in two breeding stages (%N = Percent Number; %W = Percent Weight; %IRI = Percent Index of Relative Importance)

Family	Species		April 2014		June 2014			
		%N	%W	%IRI	%N	%W	%IRI	
Cyprinidae	Rutilus rutilus	36.51	45.31	53.42	39.25	44.10	51.02	
	Cyprinus carpio	6.75	7.96	2.47	15.36	27.6	23.58	
	Blicca bjoerkna	_	_	_	0.34	3.97	0.09	
	Carassius carassius	_	_	_	0.68	_	_	
	Scardinius erythrophthalmus	0.40	0.04	0.01	0.34	0.86	0.02	
	Abramis brama	0.40	0.01	0.01	0.34	0.01	0.01	
	Leuciscus idus	0.40	0.03	0.01	0.68	1.43	0.04	
Percidae	Perca fluviatilis	43.05	16.68	37.74	35.49	20.28	23.55	
	Gymnocephalus cernuus	12.51	3.28	6.32	7.51	2.02	1.60	

Family	Species		Edge		Center			
		%N	% <i>W</i>	%IRI	%N	%W	%IRI	
Cyprinidae	Rutilus rutilus	29.61	51.90	48.72	54.39	57.64	66.22	
	Cyprinus carpio	16.76	23.64	24.15	13.16	18.34	13.96	
	Blicca bjoerkna	0.56	4.65	0.18	_	_	_	
	Carassius carassius	0.56	0.05	0.02	0.88	0.06	0.04	
	Scardinius erythrophthalmus	_	_	_	0.88	2.15	0.15	
	Abramis brama	0.56			_	_	_	
	Leuciscus idus	_	_	_	1.75	1.43	0.16	
Percidae	Perca fluviatilis	39.66	14.06	22.67	28.95	20.43	19.46	
	Gymnocephalus cernuus	12.29	2.36	4.12	_	_	_	

Table 3. Diet of *P. carbo sinensis* in the Dzierżno-Duże Reservoir in two parts of the colony (%N = Percent Number; %W = Percent Weight; %IRI = Percent Index of Relative Importance)

the proportion of fish species preyed on in the cormorant diet between the edge and the centre were found ($\chi 2 = 33.83$, df = 8, p <0.0001). Average total length of *R. rutilus* was 14.9 cm (SD ±5.1, n =58) at the edge and 10.9 cm in the centre of the colony (SD ±5.2, n = 65). For *P. fluviatilis*, the average total length was 9.3 cm (SD ±1.1, n = 58) at the edge 9.8 cm (SD ±2.3, n = 143) in the centre. No significant differences in fish length between colony parts were found (Mann-Whitney U test, U = 0.166, p <0.05).

In both parts of the colony the analysed roach (*R. ru-tilus*) showed biomass (g) values greater than 50%, while perch (*P. fluviatilis*) reached lower values (Table 3).

Discussion

The breeding colony of cormorants was established in 1994 in the Dzierżno-Duże Reservoir (southern Poland). Twenty three nests were counted in 2000 and 106 in 2001 (Profus et al. 2002). The peak number of cormorants (2000 ind.) was recorded in October 2007 (Szlama and Profus 2008).

In this reservoir the diet of the Great Cormorant was investigated through the analysis of the pellets, produced once per day, usually during the hours of rest (Cherubini and Mantovani 1997), which contain the remains of fish consumed (Veldkamp 1995).

The narrow niche breadth (*B*_i) was linked to the abundance and the behaviour of the main fish species present in the reservoir. The trophic spectrum was dominated almost exclusively by freshwater fish species, particularly those belonging to the Cyprinidae family, such as *R. rutilus*, *C. carpio*, and *P. fluviatilis* and *G. cernuus* belonging to the Percidae family, as also stated in previous works carried out in the freshwater bodies of the southern Poland (Kostecki 2000). Moreover, among the other fish species preyed on by the cormorants, crucian carp *C. carassius*, rudd *S. erythrophthalmus* and nase *Chondrostoma nasus* were considered as prey of minor importance.

The study showed how the Great Cormorant is an opportunistic, fish preying species. The diet was composed almost exclusively of a relatively limited number of species (stenophagous). It can generally be stated that it reflects the composition of the ichthyological communities inhabiting the Dzierżno-Duże Reservoir. The high abundance of species, such as those belonging to the Cyprinidae and Percidae families, combined with their typical gregarious behaviour (travelling in schools), could increase the predatory success of the cormorants, which furthermore, developed a social feeding strategy (Hughes et al. 1999). The large fish schools could also be more easily identified by the birds during flight (Wittenberger and Hunt 1985), which would be followed by other individuals to the feeding areas (Burger 1997).

Species composition and fish size in the cormorant diet differed between the studied years. This can probably be explained by changes in fish species and age structure in the fish community. Great differences in fish community structure and cormorant diet between years were found in Lake Ymsen (Sweden) (Engström and Jonsson 2003) and in Mistras lagoon (Central-Western Sardinia (Buttu et al. 2013).

The low values of the Levin (B_i) and Shannon (H') indexes showed a limited trophic spectrum in the diet. The feeding habits were effectively composed almost exclusively of Osteichthyes. Differences were also recorded during the breeding stages reflecting the requirements of chicks. During a breeding season younger chicks require smaller rather than larger and older fish. Smaller chicks that are mainly distributed in the centre of the colony prefer smaller fish that are easier to digest.

The main prey in the diet varied during different chick rearing periods in the colony found in Ramsat (Iran) (Bararti 2013). The biomass of the prey varied seasonally as a result of chick growth and increasing food requirements during the study period (Bararti 2013).

Early arrival at the breeding sites can be advantageous and should favour wintering at sites as close as possible to the breeding grounds (Van Eerden and Munsterman 1995). We found no differences in fish size between different parts of the colony (centre and edge). Reproduction success per individual in the Vorso colony (Denmark) did not decrease with increasing distance to the wintering area (Bregnballe et al. 2006).

Our results revealed great differences in the diet (fish species and size) of the Great Cormorant between years, breeding stages and parts of colony. These results indicate that the impact of a cormorant colony on fish assemblages is not always the same and depends of a variety of factors besides fish availability.

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References

- Bararti A., 2013, Diet and growth of chicks of the Great Cormorant, *Phalacrocorax carbo, at Ramsar*, northern Iran (Aves: Phalacrocoracidae), Zool. Middle East 46(1): 29–36.
- Bearhop S., Thompson D.R., Waldron S., Russell I.C., Alexander G., Furness R.W., 1999, Stable isotopes indicate the extent of freshwater feeding by cormorants *Phalacrocorax carb*o shot at inland fisheries in England, J. Appl. Ecol. 36(1): 75–84.
- Blumenbach J.F., 1798, 25. *Pelecanus Sinensis*, [in:] Abbildungen naturhistorischer Gegenstände. Vol. 3: Nro 21–30, J.Ch. Dietrich, Göttingen.
- Bregnballe T., Frederiksen M., Gregersen J., 2006, Effects of distance towintering area on arrival date and breeding performance in Great Cormorants *Phalacrocorax carbo*, Ardea 94(3): 619–630.
- Burger A.E., 1997, Arrival and departure behaviour of Common murres (Uria aalge) at colonies: evidence for an information halo?, Colon. Waterbirds 20(1): 55–65.
- Buttu S., Mulas A., Palmas F., Cabiddu S., 2013, Diet and Impact of *Phalacrocorax carbo sinensis* (AVES, PHALA-CROCORACIDE) on Transitional Environments in Central-Western Sardinia, Transiti. Water Bull. 7(2):17–27.
- Carrassón M., Matallanas J., Casadevall M., 1997, Feeding strategies of deep-water morids on the western Mediterranean slope, Deep Sea Res. 44(9–10): 1685–1699.
- Carss D.N., 2003, Reducing the conflict between cormorants and fisheries on a pan-European scale. REDCAFE. Final Report, Centre for Ecology and Hydrology, Banchory, 169 pp.
- Čech M., Čech P., Kubečka J., Prchalová M., Draštík V., 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.
- Cherubini G., Mantovani R., 1997, Variability in the results of Cormorant diet assessment by using indices for otolith digestion, Suppl. Ric. Biol. Selvaggina 26: 239–246.
- Cortés E., 1997, A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes, Can. J. Fish. Aquat. Sci. 54(12): 726–738.
- Cramp S., Simmons K.E.L., 1977, Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. 1: Ostrich to Ducks, Oxford University Press, Oxford, 732 pp.
- Dirksen S., Boudewijn T.J., Noordhuis R., Marteijn E.C.L., 1995, Cormorants *Phalacrocorax carbo sinenesis* 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.
- [EC] European Commission, 1997, Commission Directive 97/49/EC of 29 July 1997 amending Council Directive 79/409/EEC on the conservation of wild birds, Offic. J. Eur. Union L223 40: 9–17.
- [EEC] European Economic Community, 1979, 79/409/EEC Council Directive of 2 April 1979 on the conservation of wild birds, Offic. J. Eur. Union L103 22: 1–30.
- Engström H., Jonsson L., 2003, Great Cormorant *Phalacro-corax carbo sinensis* diet in relation to fish community structure in a freshwater lake, Vogelwelt 124 (Suppl.): 187–196.
- Gagliardi A., Martinoli A., Preatoni D., Wauters L.A., 2007, From mass of body elements to fish biomass: a direct method to qualify food intake of fish eating birds, Hydrobiologia 583: 213–222.
- Grémillet D., Kuntz G., Delbart F., Mellet M., Kato A., Robin J.P., Chaillon P.E., Gendner J.P., Lorentsen S.H., Le Maho Y., 2004, Linking the foraging performance of a marine predator to local prey abundance, Funct. Ecol. 18(6): 793–801.
- Gwiazda R., Amirowicz A., 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?, Pol. J. Ecol. 58(4): 783–792.
- Hartman K.J., Margraf F.J., 1992, Effects of prey and predator abundances on prey consumption and growth of walleyes in western Lake Erie, Trans. Am. Fish. Soc. 121: 245–260.
- Hobson K.A., Knapton R.W., Lysack W., 1989, Population, diet and reproductive success of Double-crested Cormorants breeding on Winnipegosis, Manitoba, in 1987, Colon. Waterbirds 12(2): 191–197.
- Horoszewicz L., 1960, Wartości kości gardłowych dolnych (ossapharyngea interiora) jako kryterium gatunkowego oznaczania ryb karpiowatych /Cyprynidae/ (The value of lower pharyngeal bones (ossa pharyngea interiora) as species criteria for defining fish of the Cyprinidae family), Rocz. Nauk Roln. B 75(2): 237–256 (in Polish).

- Hughes B., Bevan R.M., Bowler J.M., Still L., Carss D.N., Marquiss M., Hearn R.D., Bruce J., 1999, Feeding Behaviour of Fish-Eating Birds in Great Britain. Report to the Department of the Environment, Transport and Regions, London, 249 pp.
- Johnsgard P.A., 1993, Cormorants, Darters and Pelicans of the world, Smithsonian Inst. Press, Washington, 445 pp.
- Keller T., 1995, Food of Cormorants *Phalacrocorax carbo sinensis* wintering in Bavaria, southern Germany, Ardea 83: 185–192.
- Keller T., Vordermeier T., von Lukowicz M., Klein M., 1997, The impacts of Cormorants on the fish stocks of several Bavarian water bodies with special emphasis on the ecological and economical aspects of fisheries, Suppl. Ric. Biol. Selvaggina 26: 295–311.
- Kostecki M., 2000, Zawiesina jako element zanieczyszczeń antropogennego ekosystemu wodnego na przykładzie zbiornika zaporowego Dzierżno Duże (The suspended solids as an element of pollution of anthropogenic water ecosystem for example of Dzierżno Duże dam-reservoir), Arch. Ochr. Środow. 26(4): 75–94 (in Polish).
- Lagardère J.P., 1975, Rècherches sur l'alimentation descrevettes bathypelagiques du talus continental du Golfe de Gascogne (Studies on feeding bathypelagic shrimps of the continental slope of the Bay of Biscay), Rev. Trav. Inst. Péches Marit. 39(2): 213–229 (in French, English summary).
- Lauzanne L., 1982, Les Orestias (Pisces, Cyprinodontidae) du Petit lac Titicaca (Orestias (Pisces, Cyprinodontidae) in Lesser Lake Titicaca), Rev. Hydrobiol. Trop. 15(1): 39–70 (in French, English summary).
- Lehikoinen A., 2005, Prey-switching and diet of the Great Cormorant during the breeding season in the Gulf of Finland, Waterbirds 28(4): 515–515.
- Leopold M.F., van Damme C.J.G., van der Veer H.W., 1998, Diet of cormorants and the impact of cormorant predation on juvenile flatfish in the Ducht Wadden Sea, J. Sea Res. 40(1–2): 93–107
- Levins R., 1968, Evolution in Changing Environments, Princeton University Press, Princeton, 132 pp.
- Lindell L., Mellin M., Musil P., Przybysz J., Zimmerman M., 1995, Status and population development of breeding Cormorants *Phalacrocorax carbo sinensis* of the central European flyway, Ardea 83(1): 81–92.
- Lindell L., 1997, Food composition of cormorants *Phalacrocorax carbo sinensis* in Sweden, Suppl. Ric. Biol. Selvaggina 26: 163–171.
- Liordos V., Goutner V., 2008, Habitat and temporal variation in the diet of Great Cormorant nestlings in Greek colonies, Waterbirds 31(3):424–437
- Martyniak A., Terleck J., Boroń S., Hliwa P., Sza-Mańska U., Gabrś B., Romaniewicz A., 1997, Diet composition of cormorants *Phalacrocorax carbo sinensis* from pellets collected at Kąty Rybackie colony, northern Poland, Suppl. Ric. Biol. Selvaggina 26: 505–510.

- Martyniak A., Wziątek B., Szymańska U., Hliwa P., Terlecki J., 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.
- Mous P.J., Dekker W., De Leeuw J.J., van Eerden M.R., van Densen W.L.T., 2003, Interactions in the utilization of small fish by piscivorous fish and birds and the fishery in Ijsselmeer, [in:] Cowx I.G. (ed.) Interactions between fish and birds: implications for management, Blackwell, Oxford: 84–118.
- N'da K., 1992, Regime alimentaire du rouget de roche *Mullus surmeletus* (Mullidae) dans le nord du golfe de Gascogne (Feeding habits of the red mullet (*Mullus surmuletus* (Mullidae), from the north of the Bay of Biscay), Cybium 16: 159–168 (in French).
- Profus P., Ostański M., Szlama D., 2002, Awifauna zbiornika retencyjnego Dzierżno Duże na Górnym Śląsku. Cz. II. Powstanie i rozwój kolonii kormorana czarnego *Phalacrocorax carbo sinensis* (The avifauna of the Dzierżno Duże retention reservoir in Upper Silesia. Part II. Origin and development of the *Phalacrocorax carbo sinenesis* colony), Chrońmy Przyr. Ojcz. 58(3): 29–37 (in Polish, English summary).
- Platteeuw M., Koffijberg K., Dubbeldam W., 1995, Growth of cormorant *Phalacrocorax carbo sinensis* chicks in relation to brood size, age ranking and parental fishing effort, Ardea 83(1): 235–245.
- Rzętała M.A., Jaguś A., Rzętała M., 2013, Samooczyszczanie wód w procesie tworzenia form deltowych (Self-purification of waters during creation of delta forms), Rocz. Ochr. Śr.15(1): 2510–2525 (in Polish, English summary).
- Shannon C.E., Weaver W., 1949, The Mathematical Theory of Communication, University of Illinois Press, Urbana, 125 pp.
- Szlama S., Profus P., 2008, Awifauna zbiornika retencyjnego Dzierzno Duże na Gornym Slasku. Cz.3. Znaczenie zbiornika i jego otoczenia dla przelotów i zimowania ptaków (The avifauna of the Dzierzno Duze retention reservoir in the Upper Silesia. Part 3. The importance of the reservoir and its surroundings for migrating and wintering birds), Chrońmy Przyr. Ojcz. 66(6): 3–48 (in Polish, English summary).
- Sokal R.R., Rohlf F.J., 1987, Introduction to biostatistics, W.H. Freeman & Co., New York, 363 pp.
- Stempniewicz L., Martyniak A., Borowski W., Goc M., 2003, Fish stocks, commercial fishing and cormorant predation in the Vistula Lagoon, Poland, [in:] Cowx I.G. (ed.) Interactions between fish and birds: implications for management, Blackwell, Oxford: 51–64.
- van Eerden M.R., Gregersen J., 1995, Long-term changes in the northwest European population of Cormorants *Phalacrocorax carbo sinensis*, Ardea 83(1): 61–79.
- van Eerden M.R., Munsterman M. J., 1995, Sex and age dependent distribution in wintering Cormorants *Phala-*

- crocorax carbo sinensis in Western Europe, Ardea 83(1): 285–297.
- van Eerden M.R., Voslamber B., 1995, Mass fishing by cormorants *Phalacrocorax carbo sinenesis* at Lake IJseelmeer, The Netherlands: a recent and successful adaptation to a turbid environment, Ardea 83(1): 199–212.
- Veldkamp R., 1995, The use of chewing pads for estimating the consumption of cyprinids by Cormorants *Phalacroco-rax carbo*, Ardea 83(1): 135–138.
- Vetemaa M., Eschbaum R., Albert A., Saks L., Verliin A., Jurgens K., Kesler M., 2010, Changes in fish stocks in an Estonian estuary: overfishing by cormorants?, ICES J. Mar. Sci. 67(9): 1972–1979.
- Wanless S., Corfield T., Harris M.P., Buckland S.T., Morris J.A., 1993, Diving behaviour of the Shag *Phalacrocorax aristotelis* (Aves: Pelecaniformes) in relation to water depth and prev size, J. Zool. Lond. 231(1): 11–25.

- Wittenberger J.F., Hunt G.L., 1985, The adaptive significance of coloniality in birds, Avian Biol. 8: 1–78.
- Wojczulanis-Jakubas K., Minias P., Kaczmarek K., Janiszewski T., 2013, Late-breeding Great Cormorants *Phalacrocorax carbo sinensis* produce fewer young of the more vulnerable sex, Ibis 155(3): 626–631.
- Wziątek B., Martyniak A., Szymańska U., Kozłowski J., Dostatni D., 2003, Composition of the Great Cormorant *Phalacrocorax carbo sinensis* diet in the Drawa National Park, NW-Poland, Vogelwelt 124(Suppl.): 291–295.
- Zar J.H., 1996, Biostatistical analysis, Prentice Hall, Upper Saddle River, 662 pp.
- Zijlstra M., Van Eerden M.R., 1995, Pellet production and the use of otoliths in determining the diet of cormorants *Phalacrocorax carbo sinensis*: trials with captive birds, Ardea 83(1): 123–131.