Size Selectivity in Summer and Winter Diets of Great Cormorant (*Phalacrocorax carbo*): Does it Reflect Season-Dependent Difference in Foraging Efficiency?

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Abstract.—Diet of the Great Cormorant (*Phalacrocorax carbo*) was studied using regurgitated pellets, individual fish bones and fish remains collected from below roosting trees at Želivka and Slapy Reservoirs, Czech Republic, during summer, a warm winter and a cold winter. Both reservoirs have the same trophic status and similar fish assemblages. Using diagnostic bones (*os pharyngeum, dentale, praeoperculare*) and our own linear regression equations relating dimensions of the diagnostic bone and fish total length (L_T), a total of 2,055 fish of 18 species and four families were identified in the diet of Great Cormorants and their size was reconstructed. Both fish total length and weight differed significantly between seasons being, on average, 12.0 cm and 30 g during summer, 18.3 cm and 109 g during a warm winter and 22.8 cm and 157 g during the cold winter. The average weight of fish taken by Great Cormorants significantly increased with decreasing air and water temperature. The contribution of the dominant "large growing", torpedo-shaped fish species in the diet of Great Cormorants dramatically increased from summer to the cold winter. In contrast, the contribution of dominant "small growing", torpedo-shaped species, or humped body-shaped species, showed completely the opposite tendency. Great Cormorants seem to consume all fish of appropriate size that they are able to catch in summer and select for larger fish in winter. Thus, the winter elevation of foraging efficiency described for Great Cormorants in the literature is due to capturing larger fish not to capturing more fish. *Received 21 March 2007, Accepted 9 March 2008.*

Key words.—*Alburnus alburnus*, diagnostic bones, *Leuciscus cephalus*, *Perca fluviatilis*, foraging efficiency, prey size, regurgitated pellets, *Rutilus rutilus*, Slapy Reservoir, Želivka Reservoir.

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The Great Cormorant (*Phalacrocorax carbo*) is one of the most important avian fish predators both in marine (e.g., Barrett *et al.* 1990; Leopold *et al.* 1998; Johansen *et al.* 1999, 2001; Lorentsen *et al.* 2004) and freshwater (e.g., Suter 1995, 1997; Keller 1998; Engström 2001; Liordos and Goutner 2007) ecosystems. Moreover, recent studies have revealed that among endotherms the Great Cormorant is also the most efficient fish predator. Prey capture rate of this bird was estimated to be 9.0 g min^{-1} for females and 15.2 g min^{-1} for males in summer (Grémillet 1997) and nearly 60 g min^{-1} for both sexes in winter (Grémillet *et al.* 2001). Such a high predatory efficiency is a necessary result of a trade-off between time spent diving into cold water (1-10°C), very limited body insulation, maintaining a high body temperature (42.3°C) and balancing of daily energy requirements (Grémillet *et al.* 2001), since high energy losses during winter do not seem to be compensated for by an increase in fish intake (Johansen *et al.* 2001). The winter elevation of foraging efficiency depends critically upon dense, highly predictable prey stocks allowing birds to gain sufficient energy during an extremely short dive session (usually one per day) lasting, on average, only 9 min (Grémillet *et al.* 2001).

In principle, wintering Great Cormorants could increase their catch per unit of effort (C.P.U.E.) in two different ways. Either they could catch more fish or they could catch larger fish compared with the summer situation. The former is partly possible by choice of appropriate fishing localities, such as overstocked carp ponds (Adámek and Kortan 2002), otherwise it is unlikely (Johansen *et al.* 2001) because it would require a miraculous enhancement of their fishing abilities. The latter would be possible if the accessibility of larger fish (measured as ability to escape from a predator) differed with season. This is possible because fish, as ectotherms, significantly reduce their movement activity in winter (for review see e.g., Wootton 1998).

The aim of this study was to test the hypothesis that, in winter, Great Cormorants increase their C.P.U.E. in order to maintain daily food intake, while reducing their daily fishing period, by catching larger fish compared to those caught in summer. This was tested *in situ* on two large canyon-shaped reservoirs, which have the same trophic status and similar fish fauna, but are used by Great Cormorants during different periods of the year.

STUDY AREA

The study was carried out at two Great Cormorant roosting places on two large meso- to eutrophic Czech reservoirs—Želivka Reservoir and Slapy Reservoir (Fig. 1). The Želivka Reservoir, with an area of 1,670 ha (built in 1976, length 38 km, maximum depth 55 m, volume 246×10^6 m^3, 60 km south-east of Prague) is the largest water-supply reservoir in Central Europe. Entry into the reservoir's first protected zone is prohibited. Because of a very low mean annual inflow of <7 m^3 s^{-1}

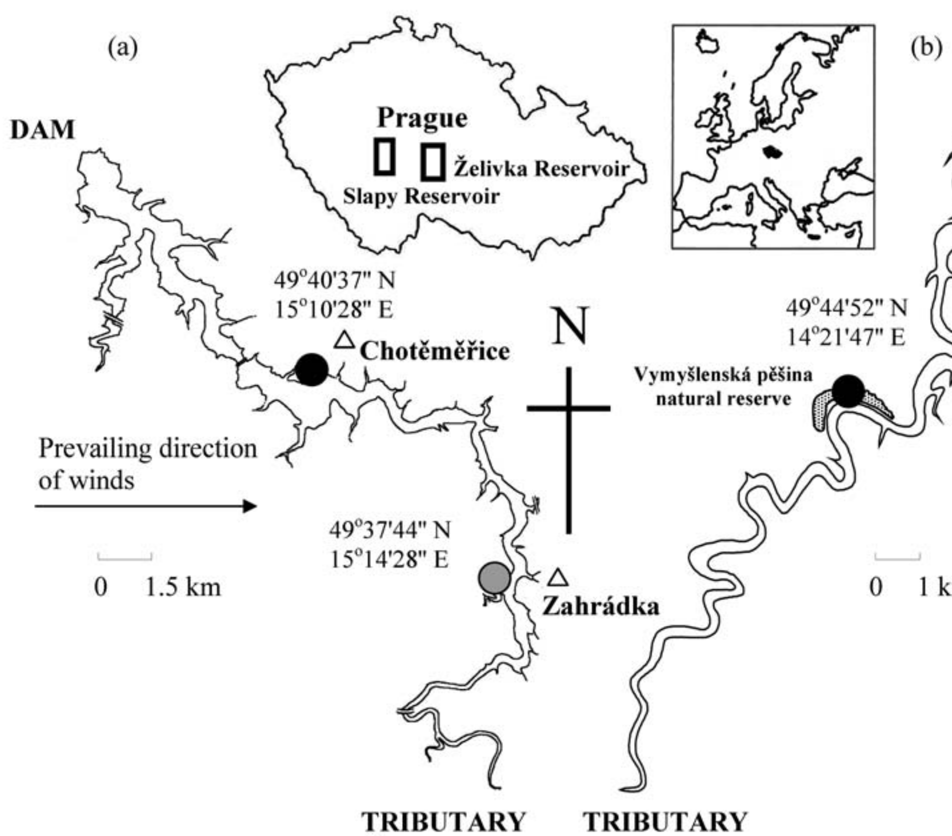

Figure 1. A map of (a) Želivka Reservoir and (b) Slapy Reservoir and their locations in the Czech Republic. Black dots show the roosting places of Great Cormorant (*Phalacrocorax carbo*) where regurgitated pellets, fish bones and sporadic fish remains were collected (latitude and longitude is given for each roosting place). The gray dot (Želivka Reservoir) indicates the concurrent roosting place where food remains could not be collected due to the extremely difficult access (Pines on a steep rocky bank). Flocks of Great Cormorants regularly used both roosting places. In both roosts studied the regurgitated pellets, fish bones and remains are, immediately after the roosting season (frequently just during the roosting season), scavenged by Red Foxes (*Vulpes vulpes*), Feral Pigs (*Sus scrofa*) and Pine Martens (*Martes martes*) in the manner described by Čech and Hladík (2005). Contamination of the samples by regurgitated pellets and fish remains from other periods of the year (Želivka) or from previous years (both reservoirs) is therefore negligible. Note that all roosting places are open to the south or southeast and they are well protected against winds coming from the west.

and, resulting from that, a high theoretical retention time of 424 days and, in addition, its relatively high altitude (375 m.a.s.l.), the reservoir is usually covered by ice from mid-December to the end of March. The fish assemblage of Želivka Reservoir comprises 19 species and one hybrid, but only a few species, Roach (*Rutilus rutilus*), Bleak (*Alburnus alburnus*), Bream (*Abramis brama*) and European Perch (*Perca fluviatilis*) occur in ecologically significant numbers, comprising, in the long term, >95% of the fish stock (Čech *et al.* 1998; Prchalová *et al.* 2005; Prchalová *et al.* 2006, 2008).

The Slapy Reservoir has an area of 1,392 ha (built in 1954, length 42 km, maximum depth 58 m, volume 269 × 10^6 m^3, 40 km south of Prague) and is the seventh reservoir (downstream) in the system of the Vltava River cascade. Its location close to Prague results in enormous recreational pressure (water sports, angling) from May to at least October. For most of the winter, this reservoir is filled with relatively warm, hypolimnetic water (7.7-8.5°C; Čech *et al.* 2007a) discharged from the reservoirs upstream. Because of its high mean annual inflow of 85 m^3 s^{-1}, resulting in a theoretical retention time of only 38.5 days, and low altitude (271 m.a.s.l.) (Hrbáček and Straškraba 1966), even in severe winters (winter 2005/06 lasted for 4.5 months) the reservoir is covered by ice for less than two weeks. The fish assemblage of Slapy Reservoir comprises at least 13 species, but the majority of the fish stock (>97%) is composed of Roach, Bleak, Bream, European Perch and Ruffe (*Gymnocephalus cernuus*) (Draštík *et al.* 2004, 2006; Čech *et al.* 2005).

The fish communities of relatively old (>25 y) Central European reservoirs are apparently not changing dramatically (species composition, size spectra) during the season and from year to year (Říha *et al.* 2008). The only exception is the community of young-of-the-year fish much less than five cm total length (L_T) (Čech *et al.* 2005, 2007a, b; Čech and Kubečka 2006), which are, however, usually not targeted by Great Cormorants (e.g., Barrett *et al.* 1990; Adámek 1991; Leopold *et al.* 1998; Johansen *et al.* 1999; Lorentsen *et al.* 2004). So, it is not possible to assume that a different fish community is available to summer and winter flocks of Great Cormorants foraging on Želivka and Slapy Reservoirs.

At both reservoirs, Great Cormorants roost on Pines (*Pinus sylvestris*) and Oaks (*Quercus robur*) on a steep bank, close to Chotěměřice and Zahrádka village (Želivka Reservoir) and below the Vymyšlenská pěšina natural reserve (Slapy Reservoir) (Fig. 1). The Great Cormorants exploit Želivka Reservoir in summer and autumn up to the start of continuous ice-cover (M. Kavka and J. Křivský, unpubl. data). In contrast, Slapy Reservoir is used by Great Cormorants as a foraging and roosting area in winter when the overall recreational pressure drops dramatically (P. Čech and M. Čech, pers. data). There are no breeding colonies of Great Cormorants at both reservoirs, moreover, there are no breeding colonies at least 60 km each direction off both reservoirs.

Based on the above observations, the samples analyzed correspond to the period 1 July to 30 September 2003 (Želivka Reservoir; up to 90 roosting birds) referred to as "summer" and from 16 December 2005 to 15 March 2006 (Slapy Reservoir; *c.* 60 roosting birds) referred to as "cold winter" (Table 1). Extremely warm weather during winter 2006/07 (warmest winter since year 1922; Czech Hydrometeorological Institute, unpubl. data) prevented ice covering Želivka Reservoir and enabled roosting and foraging of over 150 Great Cormorants there (P. Čech and M. Čech, pers. data). However, the roosting place also became a highly exploited scavenging area. Feral Pigs (*Sus scrofa*) periodically visited this area, dug up the ground and ate practically all the regurgitated pellets, bones and fish remains. The sample analyzed from winter 2006/07, referred to as "warm winter", is therefore undoubtedly not more than one month old and corresponds to January 2007 (Table 1).

Table 1. Mean, SD, minimum and maximum air and water temperatures in Želivka Reservoir (summer 2003, warm winter 2007) and in Slapy Reservoir (cold winter 2005/06). The winter water temperature was taken from the whole water column, since fish could be evenly found throughout the water column during winter (Eckmann and Imbrock 1996) while the summer water temperature was taken from the epilimnion exclusively (up to the depth of 3-11 m), since the majority of fish occupy this part of the water column at that time (Čech and Kubečka 2002; Vašek *et al.* 2004; Prchalová *et al.* 2008). Both air and water temperatures differed significantly between reservoirs and seasons ($ANOVA_{air}$: $F_{2, 640} = 1497.09$, $P < 0.001$; $ANOVA_{water}$: $F_{2, 36} = 251.09$, $P < 0.001$). Result of the Tukey test indicated by the asterisks.

	Želivka Reservoir		Slapy Reservoir
Parameter	summer	warm winter	cold winter
Air temperature (°C)[a]			
Mean ± S.D.	18.5 ± 6.0***	4.7 ± 5.0***	-2.5 ± 4.3***
Min. – Max.	2.3-36.8	-7.2 – 13.9	-16.6 – 9.1
Water temperature (°C)[b,c]			
Mean ± S.D.	22.1 ± 3.4***	6.1 ± 0.8*	3.1 ± 1.2*
Min. – Max.	17.4 – 26.2	4.3 – 7.0	2.2 – 5.4

[a]Czech Hydrometeorological Institute (unpubl. data), measured three times a day.
[b]Vltava River Authority (unpubl. data from Želivka Reservoir), measured monthly.
[c]Biology Centre AS CR, Institute of Hydrobiology (unpubl. data from Slapy Reservoir), measured in three weeks interval.
*P < 0.05; ***P < 0.001.

METHODS

Composition and size of fish prey in the diet of Great Cormorants was investigated from regurgitated pellets, individual bones and sporadic fish remains collected below the roosting trees during a single visit to each colony on 30 September 2003 and on 3 February 2007 (Želivka) and on 8 April 2006 (Slapy). About 200 m^2 of the ground was searched at Želivka Reservoir and about 250 m^2 at Slapy Reservoir, from which 2,500 ml (Želivka 2003), 3,500 ml (Želivka 2007) and 2,000 ml (Slapy 2005/06) of food remains were collected. Whole regurgitated material was immersed for one week in concentrated detergent solution, then washed through a sieve (mesh size one mm), dried at room temperature and analyzed under a binocular magnifying glass (magnification 8-16×).

To identify the species and size of fish prey, a reference collection of diagnostic bones was constructed for each of the potential prey species. Reference fish were taken from gill net and seine net catches from Římov Reservoir in the years 2000-2006 (Czech Republic). Similar to Želivka and Slapy, Římov Reservoir belongs to the Vltava River basin, has the same trophic status and a similar fish assemblage (Vašek *et al.* 2004). This matches well the requirement for the back calculation of fish length from the measurement of diagnostic bones given in the work of Radke *et al.* (2000). In total, 408 fish were measured (total length, L_T, to the nearest 0.1 cm), boiled, dissected and the diagnostic bones, selected according to Reynolds and Hinge (1996) and Čech and Čech (2006), were measured to the nearest 0.1 mm (Appendix 1). Pharyngeal bones (*os pharyngeum*) were selected for cyprinid species (Cyprinidae), lower jaws (*dentale*) for Northern Pike (*Esox lucius*) and percid species (Percidae) and preopercular bones (*praeoperculare*) for percid species. The measurements selected were the pharyngeal bone tip, PhT, for cyprinid species, dental length, DeL, for Northern Pike and percid species and the preopercular gape, PpG, for percid species (Appendix 1). From the reference material collected, a linear regression equation was established for each prey species between the measured dimension of the diagnostic bone and L_T (Appendix 2). Mass estimates for the fish prey were obtained by using a length-weight regression equation for each fish species from either Želivka (Prchalová *et al.* 2005, 2006) or Římov (J. Kubečka and M. Prchalová, unpubl. data) Reservoir.

Data were analyzed using linear regression and ANOVA. Tukey HSD post-hoc comparisons for unequal N (Tukey test) were used after ANOVA for detailed identification of significant differences between localities and seasons.

RESULTS

In Želivka Reservoir during summer 2003, regurgitated diet remains of Great Cormorants included 729 fish (after pairing the diagnostic bones) of 11 fish species and 3 families (Cyprinidae, Esocidae, Percidae). Roach, Bream, Bleak and European Perch represented 97.4% (numerically) of the diet (Table 2). From the dominant species, Roach were taken in the length range 5-35 cm (average L_T 10.8 cm), Bleak in the length range 11-18 cm (average L_T 13.4 cm) and European Perch in the length range 8-29 cm (average L_T 13.5 cm). The largest fish taken by the Great Cormorants was a 36 cm Northern Pike, the heaviest was a 575 g Roach. Fish ≤20 cm L_T comprised 93.3% of the Cormorants' diet.

In Želivka Reservoir during the warm winter 2007, the regurgitated diet remains of Great Cormorants included 722 fish of 17 fish species and 4 families (Cyprinidae, Esocidae, Salmonidae, Percidae). Roach, Bream, Bleak and European Perch represented 80.7% of the diet (Table 2). From the dominant species, Roach were taken in the length range 5-38 cm (average L_T 18.2 cm), European Perch in the range of 6-31 cm (average L_T 17.2 cm), European Chub (*Leuciscus cephalus*) 12-35 cm (average L_T 19.8 cm) and Bleak 7-18 cm (average L_T 13.4 cm). The largest fish taken by the Great Cormorants was a 39.5 cm Northern Pike, the heaviest was a 755 g Roach. Fish ≤20 cm L_T comprised 67.0% of the Cormorants' diet.

In Slapy Reservoir during the cold winter 2005/06, the regurgitated diet remains of Great Cormorants included 604 fish of 13 fish species and 3 families (Cyprinidae, Esocidae, Percidae). Roach, Bream, Bleak, European Perch and Ruffe represented 90.6% of the diet (Table 2). From the dominant species, Roach was taken in the length range 6-35 cm (average L_T 22.9 cm), European Perch in range 11-29 cm (average L_T 21.2 cm) and European Chub 7-31 cm (average L_T 24.3 cm). The largest fish taken by Great Cormorants was a 38 cm Northern Pike, the heaviest was a 575 g Roach. Fish ≤20 cm L_T composed only 26.5% of Cormorants' diet.

Size of fish captured and ingested by the Great Cormorants differed significantly between reservoirs and seasons (ANOVA: $F_{2,2052} = 347.03$, $P < 0.001$) being on average 22.8 cm L_T in the case of Slapy Reservoir (cold winter), 18.3 cm L_T in the case of Želivka Reservoir (warm winter) and only 12.0 cm L_T in Želivka Reservoir (summer) (Tukey test: $P < 0.001$ for each of the two tested values; Fig. 2). Similarly, the weights of fish captured and ingested by the Great Cormorants dif-

Table 2. Fish species composition in the diet of Great Cormorants (*Phalacrocorax carbo*) hunting on Želivka Reservoir (summer 2003, warm winter 2007) and on Slapy Reservoir (cold winter 2005/06).

	Želivka Reservoir				Slapy Reservoir	
	summer		warm winter		cold winter	
Species	n	%	n	%	n	%
Roach (*Rutilus rutilus*)	347	47.6	410	56.8	502	83.1
Bream (*Abramis brama*)	14	1.9	11	1.5	1	0.2
White Bream (*Blicca bjoerkna*)	—	—	10	1.4	6	1.0
Bleak (*Alburnus alburnus*)	231	31.7	70	9.7	5	0.8
European Chub (*Leuciscus cephalus*)	3	0.4	77	10.7	18	3.0
Asp (*Aspius aspius*)	1	0.1	3	0.4	—	—
Tench (*Tinca tinca*)	—	—	—	—	6	1.0
Common Carp (*Cyprinus carpio*)	1	0.1	9	1.2	8	1.3
Rudd (*Scardinius erythrophthalmus*)	7	1.0	2	0.3	2	0.3
Grass Carp (*Ctenopharyngodon idella*)	—	—	1	0.1	6	1.0
Gudgeon (*Gobio gobio*)	—	—	19	2.6	—	—
Nase (*Chondrostoma nasus*)[a]	—	—	2	0.3	—	—
Barbel (*Barbus barbus*)[a]	—	—	1	0.1	—	—
Trout spp. (*Salmo* spp.)[a]	—	—	1	0.1	—	—
Northern Pike (*Esox lucius*)	3	0.4	5	0.7	5	0.8
European Perch (*Perca fluviatilis*)	118	16.2	92	12.7	38	6.3
Ruffe (*Gymnocephalus cernuus*)	3	0.4	6	0.8	1	0.2
Zander (*Sander lucioperca*)	1	0.1	3	0.4	6	1.0
Total	729	100.0	722	100.0	604	100.0

[a]Species classification and size estimates of two Nase, one Barbel and one Trout spp. was done using own reference collection of diagnostic bones of these species, which originated from streams and rivers belonging to the Vltava River basin.

fered significantly between reservoirs and seasons (ANOVA: $F_{2, 2052} = 154.63$, $P < 0.001$) being on average 157 g in the case of Slapy Reservoir (cold winter), 109 g in the case of Želivka Reservoir (warm winter) and only 30 g in Želivka Reservoir (summer) (Tukey test: $P < 0.001$ for each of the two tested values). Therefore, fish consumed by the Great Cormorants in a cold winter were over 5 times heavier than the fish consumed in summer and those consumed in a warm winter were over 3.5 times heavier compared to fish consumed in summer.

The average weight of fish taken by the Great Cormorants significantly increased with decreasing air temperature (regression analysis: $y = -6.05x + 140.70$, $r^2 = 0.19$, $F_{1, 2053} = 308.91$, $P<0.001$; Fig. 3a), and decreasing water temperature (regression analysis: $y = -6.31x + 165.84$, $r^2 = 0.18$, $F_{1, 2053} = 285.99$, $P < 0.001$; Fig. 3b).

The contribution of the dominant large torpedo-shaped species, such as Roach and European Chub, in the diet of Great Cormorants dramatically increased from summer to cold winter (regression analysis: $y = 19.05x + 29.10$, $r^2 = 0.99$, $F_{1, 1} = 5376.33$, $P < 0.01$; Fig. 4, Table 2), following the decrease of air and water temperature. In contrast, the contribution of the dominant small torpedo-shaped species like Bleak, or humped-body shaped species like European Perch, in the diet of Great Cormorants revealed a completely opposite tendency (regression analysis: $y = -20.40x + 66.60$, $r^2 = 0.98$, $F_{1, 1} = 48.00$, $P = 0.09$; Fig. 4, Table 2).

DISCUSSION

Diet composition of Great Cormorants foraging on Želivka and Slapy Reservoirs was dominated by Roach and European Perch (in the case of Želivka also by Bleak) which markedly resembles their typical diet for most eutrophic lakes and reservoirs as defined by Suter (1997) and corresponds to the fish assemblage of these reservoirs (Čech *et al.* 1998, 2005; Draštík *et al.* 2004, 2006;

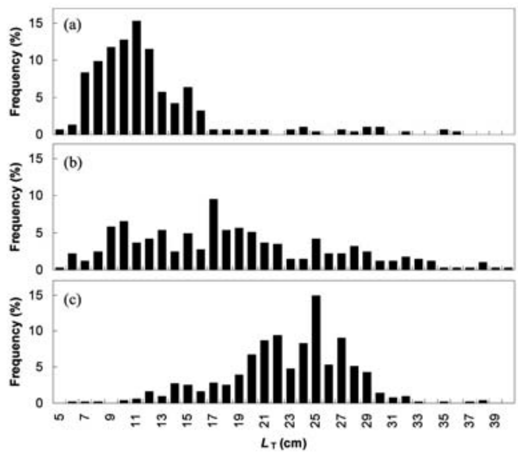

Figure 2. Frequency distributions of total length (L_T) of all fish species found in the diets of Great Cormorants (*Phalacrocorax carbo*) hunting on a) Želivka Reservoir (summer 2003; N = 729), b) Želivka Reservoir (warm winter 2007; N = 722) and c) Slapy Reservoir (cold winter 2005/06; N = 604).

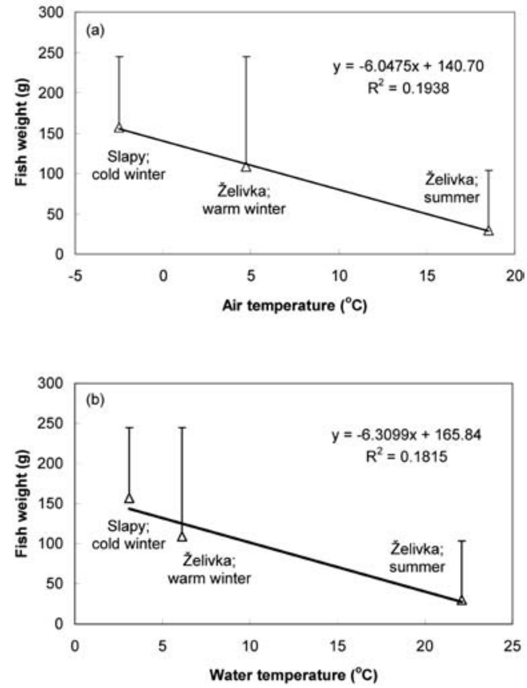

Figure 3. The relationship between a) air temperature and b) water temperature and fish weight (mean + SD in each case) recorded in the diet of Great Cormorants (*Phalacrocorax carbo*) foraging on Želivka Reservoir (summer 2003, warm winter 2007) and Slapy Reservoir (cold winter 2005/06). For temperature details see Table 1.

Prchalová *et al.* 2005, 2006, 2008). The only exception was the relatively low contribution of Bleak and European Perch in their diet at Slapy Reservoir since both species (together with Roach) strongly dominate the fish fauna of this reservoir (Draštík *et al.* 2004, 2006; Čech *et al.* 2005). However, considering the average size of fish taken by the Great Cormorants during the cold winter (22.8 cm L_T), Bleak was probably an inadequate prey since the adults rarely grow up to 20 cm L_T and their usual size in Czech reservoirs is *c.* 16 cm L_T (Prchalová *et al.* 2005, 2006).

On the other hand, due to their humped-body shape, ctenoid scales, thorns on their opercular bones and sharp hard rays in the first dorsal fin, European Perch is difficult for avian predators to swallow, especially at larger sizes (Čech and Čech 2006). Grémillet *et al.* (2006) suggest that Great Cormorants possess some means of judging the likelihood of capture. This strategy allows birds, particularly in cold water, to save time and energy by avoiding prey items perceived as energetically less rewarding or difficult to catch. If the Cormorants generally select larger fish in winter then European Perch, even though one of the dominant species in the reservoir, would clearly be an inconvenient prey (extending the handling time) and would be negatively selected. This assumption is supported by the dietary data presented here from both Želivka and Slapy Reservoirs (cf. Čech *et al.* 2005; Prchalová *et al.* 2005, 2006; Čech and Čech 2006). Moreover, while in summer the average size of European Perch taken exceeded the average size of fish taken (all prey species together), during both warm and cold winters the situation was clearly the opposite, suggesting that European Perch when caught were again suboptimal prey. At this time, the Great Cormorants strongly selected torpedo-shaped species such as Roach and European Chub, which although of larger sizes are much easier for avian predators to swallow (Čech and Čech 2006).

Grémillet (1997) estimated the prey capture rate of Great Cormorants in summer to be approx. 12 g min^{-1} (average for both sexes). In winter, however, the prey capture rate increased to nearly 60 g min^{-1} (Grémillet *et*

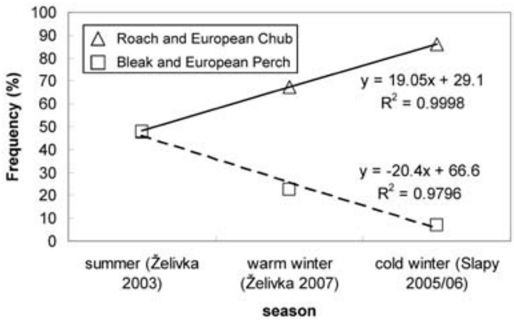

Figure 4. The contribution of the dominant "large growing" torpedo-shaped species (Roach, European Chub) in contrast to the contribution of the dominant "small growing" torpedo-shaped species (Bleak) and humped-body shaped species (European Perch) in the diet of Great Cormorants (*Phalacrocorax carbo*) hunting on Želivka Reservoir (summer 2003, warm winter 2007) and Slapy Reservoir (cold winter 2005/06). For details of the diet composition see Table 2.

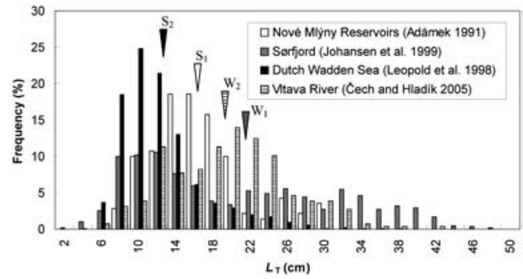

Figure 5. Frequency distributions of total length (L_T) of all fish species consumed by Great Cormorants (*Phalacrocorax carbo*) fishing in Nové Mlýny Reservoirs (summer, S_1), Sørfjord (winter, W_1), Dutch Wadden Sea (summer, S_2; flatfishes, Pleuronectiformes exclusively, composing 73% in numbers and 79% in mass of fish found in the birds' diet) and the Vltava River (winter, W_2). Arrows indicate the mean L_T of fish consumed by Great Cormorants in the individual localities. The prey size differed significantly between seasons (ANOVA: $F_{1, 4931}$ = 1236.60, P < 0.001) being much larger in winter than in summer.

al. 2001), leading to the elevation of foraging efficiency up to 5 times. In the study presented here, the average weight of fish captured and ingested by Great Cormorants during summer was 30 g (Želivka Reservoir; fish ≤20 cm L_T composed 93.3% of Cormorants' diet), while during the warm winter it was 109 g (Želivka Reservoir; fish ≤20 cm L_T composed 67.0% of Cormorants' diet) and during the cold winter 157 g (Slapy Reservoir; fish ≤20 cm L_T composed 26.5% of Cormorants' diet). This means that during one successful capture and ingestion of a fish, a Great Cormorant gains over 3.5 times more energy in a warm winter and over five times more energy in a cold winter than in summer. For that reason, these findings are in close conformity with the previous estimates of Grémillet (1997) and Grémillet *et al.* (2001). An optimal weight of Cormorant's fish prey when the air temperature reaches 0°C seems to be 140 g, while when the water temperature reaches 0°C it seems to be over 165 g.

Season-dependent size selectivity has been documented for Great Cormorants feeding in both marine and freshwater ecosystems (Fig. 5). Johansen *et al.* (2001) have shown that in Sørfjord, Norway, this species economized their midwinter energy expenditure by halving the time spent at sea, and halving the number, but doubling the mass, of each fish taken compared to the situation in late fall or early spring. Keller (1998) has noted that at Lake Ammersee, Germany, larger prey were taken in winter than in summer. In the Dutch Wadden Sea, the absolute majority of the summer diet of Great Cormorants was ≤20 cm L_T (Leopold *et al.* 1998). In Sula archipelago, Norway, the average weight of summer prey taken by Great Cormorants was 50.2 g and nearly 90% of the fish caught had weights <100 g (Lorentsen *et al.* 2004). Similarly, in the summer diet of Great Cormorants foraging on Nové Mlýny Reservoirs, Czech Republic, fish ≤20 cm L_T comprised 86.4% and the average size of fish was 15.6 cm L_T (Adámek 1991). In contrast, wintering Great Cormorants feeding in the Vltava River close to Vyšší Brod, Czech Republic, captured and ingested fish of average size 18.6 cm L_T and average weight 114 g. Fish ≤20 cm L_T still comprised 60.3% of the prey (Čech and Hladík 2005), which is very similar to the situation during the warm winter on Želivka Reservoir.

Since it is very hard to imagine that the fishing abilities of Great Cormorants dramatically increased in winter when, due to the physiological constraints, the birds are forced to reduce their foraging time to an absolute minimum (Grémillet *et al.* 2001), the only explanation for such an elevation of C.P.U.E. is due to the reduced activity of the fish (Wootton 1998). It appears that, during summer, larger fish (>20 cm L_T) are mostly able to escape, while during winter, due to the significant temperature decline, they are slow enough to be captured by the Cormorants. Especially during a cold winter, the birds are forced to catch those large fish even though it could be less comfortable to swallow them and digest them. Keeping in mind that Great Cormorants consume all fish of appropriate size that they are able to catch in summer they clearly select for larger fish in winter. In summary, therefore, it can be said that the winter elevation of foraging efficiency of Great Cormorants is due to them capturing larger fish rather than capturing more fish.

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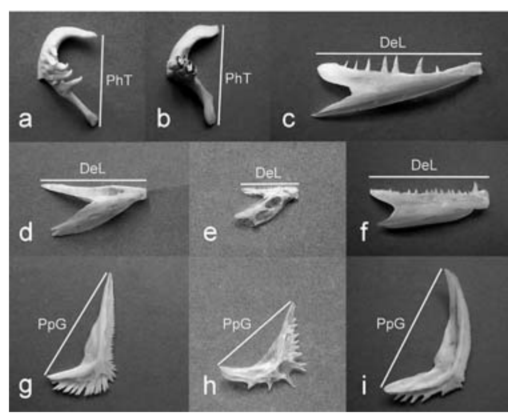

Appendix 1. Diagnostic bones of selected fish species: pharyngeal bone (*os pharyngeum*) of (a) European Chub, (b) Tench; lower jaw (*dentale*) of (c) Northern Pike, (d) European Perch, (e) Ruffe and (f) Zander; preopercular bone (*praeoperculare*) of (g) European Perch, (h) Ruffe and (i) Zander. The white line indicates the measurement. PhT, pharyngeal tip; DeL, Dental length; PpG, preopercular gape. Photo M. Čech.

Appendix 2. Regression equations of total length (L_T; cm) on bone dimensions (mm) for the 15 prey species. Numbers in parentheses represent the range of fish lengths (cm) from which the equations are derived. PhT, pharyngeal tip; DeL, dental length; PpG, preopercular gape (for details see Appendix 1).

Species	n	Equation
Roach (*Rutilus rutilus*)	31	L_T = 1.4164PhT+1.1636 r^2 = 0.9645 (5.5-38.0)
Bream (*Abramis brama*)	9	L_T = 1.7671PhT+0.244 r^2 = 0.9956 (6.7-48.0)
White Bream (*Blicca bjoerkna*)	5	L_T = 1.7206PhT+1.7419 r^2 = 0.934 (23.5-36.0)
Bleak (*Alburnus alburnus*)	33	L_T = 2.1733PhT+0.1657 r^2 = 0.9699 (7.2-23.0)
European Chub (*Leuciscus cephalus*)	83	L_T = 1.3733PhT-0.025 r^2 = 0.9883 (5.1-49.0)
Asp (*Aspius aspius*)	13	L_T = 1.4942PhT+1.1551 r^2 = 0.9923 (10.0-69.0)
Tench (*Tinca tinca*)	19	L_T = 1.3262PhT-0.3947 r^2 = 0.9919 (5.7-53.0)
Common Carp (*Cyprinus carpio*)	13	L_T = 1.1102PhT-2.8219 r^2 = 0.9854 (6.4-53.0)
Rudd (*Scardinius erythrophthalmus*)	9	L_T = 1.4894PhT+0.6513 r^2 = 0.9681 (13.5-31.0)
Grass Carp (*Ctenopharyngodon idella*)	3	L_T = 1.6925PhT-15.2 r^2 = 0.9992 (48.0-73.5)
Gudgeon (*Gobio gobio*)	7	L_T = 1.4058PhT+2.4448 r^2 = 0.9981 (4.5-13.5)
Northern Pike (*Esox lucius*)	7	L_T = 0.6981DeL+3.9125 r^2 = 0.9877 (24.5-41.0)
European Perch (*Perca fluviatilis*)	132	L_T = 1.1217DeL+1.7753 r^2 = 0.9815 (7.2-47.5) L_T = 0.8821PpG+0.9797* r^2 = 0.9903 (7.2-47.5)
Ruffe (*Gymnocephalus cernuus*)	17	L_T = 1.6758DeL-0.1998 r^2 = 0.9542 (5.6-12.5) L_T = 0.7923PpG+0.4587* r^2 = 0.9841 (5.6-12.5)
Zander (*Sander lucioperca*)	27	L_T = 1.0821DeL-1.17 r^2 = 0.9958 (5.0-51.0) L_T = 1.1815PpG-1.2726* r^2 = 0.9972 (5.0-51.0)

*These linear regressions were preferably used to calculate L_T due to the higher correlation of bone dimension with fish length.