Winter diet of great cormorant (Phalacrocorax carbo) on the River Vltava: estimate of size and species composition and potential for fish stock losses

Authors: Čech, Martin, and Vejřík, Lukáš

Source: Folia Zoologica, 60(2) : 129-142

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v60.i2.a7.2011

Folia Zool. – 60 (2): 129–142 (2011)

Winter diet of great cormorant (*Phalacrocorax carbo*) on the River Vltava: estimate of size and species composition and potential for fish stock losses

Martin ČECH* and Lukáš VEJŘÍK

Biology Centre of the Academy of Sciences of the Czech Republic, Institute of Hydrobiology, Na Sádkách 7, 370 05 České Budějovice, Czech Republic; e-mail: carcharhinusleucas@yahoo.com

Received 22 June 2010; Accepted 5 November 2010

Abstract. The winter diet of the great cormorant (*Phalacrocorax carbo*) was studied by means of examining regurgitated pellets, individual fish bones and fish remains collected from below the roosting trees in two sites on the River Vltava in Vyšší Brod and at Slapy Reservoir, Czech Republic, and by analysis of stomach contents of birds shot on the River Vltava in Prague. Using diagnostic bones (*os pharyngeum*, *dentale*, *maxillare*, *praeoperculare*) and own linear regression equations between measured dimension of the diagnostic bone and fish total length (L_T), a total of 1152 fish of 22 species and 6 families were identified in the diet of great cormorants and their sizes were reconstructed. At all three localities on the main stream of the River Vltava, roach (*Rutilus rutilus*), bream (*Abramis brama*), bleak (*Alburnus alburnus*), European chub (*Squalius cephalus*), European perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*) made up at least 74.2 % of the cormorants' diet. A great potential for fish stock losses was identified for the River Vltava at Vyšší Brod and in Prague where the loss of fish due to overwintering great cormorants was estimated to be 22 kg ha^{-1} and up to 79 kg ha^{-1} respectively, i.e. belonging among the highest ever published figures for fish withdrawal caused by great cormorants from any inland waters (carp fishponds excluded). Most probably, both great cormorants and anglers are responsible for the decrease in catches of brown trout (*Salmo trutta* m. *fario*) and grayling (*Thymallus thymallus*) from the River Vltava in Vyšší Brod.

Key words: diagnostic bones, European chub, European perch, fish withdrawal, grayling, regurgitated pellets, roach, ruffe, Slapy Reservoir, trout spp.

Introduction

The great cormorant (*Phalacrocorax carbo*) as highly efficient avian fish predator (Grémillet 1997, Grémillet et al. 2001) is able to cause serious losses to both marine (e.g. Barrett et al. 1990, Leopold et al. 1998, Johansen et al. 1999, Lilliendahl & Solmundsson 2006) and farm fisheries (Lekuona 2002) as well as to freshwater fisheries (Stewart et al. 2005). The large increase in the number of great cormorants in continental Europe since 1980 has provoked widespread conflict with both commercial and sport/recreational fisheries, which in turn has led to an upsurge in diet analyses. Excluding carp fishponds, blaming great cormorants for negative effects on wild freshwater fish populations and yields has many times had surprisingly little support in the results of dietary studies carried out in various European countries and on various types of waters (for exception see Mous 2000). Mostly, it is considered unlikely that birds impose a serious threat to either commercial or recreational fisheries, since there is only a small overlap between the cormorants' diet and valuable prey, suggesting minimal competition with human interests (e.g. Keller 1995, Keller 1998, Engström 2001, Carss & Ekins 2002, Wziątek et al. 2005, Liordos & Goutner 2007, Liordos & Goutner 2008). In the

* *Corresponding Author*

cases of eutrophic lakes and water supply reservoirs, by taking away large amounts of zooplanktivorous fish, great cormorants are, moreover, considered to have a positive influence on water quality by reducing the overexploitation of zooplankton (Dirksen et al. 1995, Veldkamp 1995, Čech 2004, Čech & Čech 2009). Besides juvenile flatfish (Pleuronectiformes) and European eel (*Anguilla anguilla*) in coastal habitats (Leopold et al. 1998, Carss & Ekins 2002), the only fish threatened by great cormorants feeding in inland waters seems to be grayling (*Thymallus thymallus*) (Suter 1997, Staub et al. 1998). However, the real effect of great cormorants on the annual yields and population dynamics of this vulnerable species is still a subject of heated debate (cf. Suter 1995, Staub et al. 1998, Suter 1998).

In the Czech Republic, excluding carp fishponds again, the main problem with great cormorants is undoubtedly concentrated on rivers below reservoirs, where secondary salmonid stretches have been found due to the discharge of relatively cold – hypolimnetic water from the reservoirs upstream (the whole year round discharge of relatively cold water, resulting, however, in ice-free conditions during winter). These river stretches are very interesting localities for both anglers (open season from mid-spring to mid-fall) and great cormorants (winter). A typical example is the River Vltava below Lipno I and Lipno II Reservoirs – i.e. the River Vltava in Vyšší Brod (Fig. 1), where the fisheries Vltava 28 and Vltava 27 are among the best Czech sport fisheries for trout spp. and grayling. Since the mid-90s these river stretches have also been visited by overwintering great cormorants (at a maximum of up to > 200 birds; K. Křivanec, unpublished data). At the same time, anglers started to blame the great cormorants for reduced yields of the two native fish species – brown trout (*Salmo trutta* m. *fario*) and grayling. Their opinion was well supported by the official catch statistics of the Czech Anglers Union. For example, in the fishery Vltava 28 the catches of grayling have decreased significantly since 1996 (regression analysis: $r^2 = 0.96$, $F_{1,5} = 129.75$, $P < 0.001$; Fig. 2) from 597 fish caught in 1996 to only 52 in 2002 (> 91 % reduction). In 2003, fishing for grayling was completely prohibited in this fishery. Similarly, the catches of brown trout have also decreased dramatically since 1999 (regression analysis: $r^2 = 0.88$, $F_{1,3} = 21.86$, $P < 0.05$; Fig. 2) from 1236 fish caught in 1999 but only 254 in 2003 (> 79 % reduction). The same trends in catches of grayling and brown trout were observed for the neighbouring fishery Vltava 27 (Czech Anglers Union, unpublished data).

The aim of this study was to analyze the winter diet of great cormorants on the River Vltava in Vyšší Brod (species and size composition) and evaluate the losses caused to the recreational fisheries (total fish consumption, fish withdrawal per ha of targeted fisheries). The results were compared with two other stretches of the River Vltava where the predation pressure and losses caused by overwintering great cormorants are supposed to be either less important (the River Vltava in Prague) or even negligible (Slapy Reservoir).

Study Area

The study was carried out at three great cormorant roosting sites on the main stream of the River Vltava, Czech Republic – the River Vltava in Vyšší Brod (*c*. 320 river km; winter 2004/05), Slapy Reservoir (*c*. 108 r. km; winter 2005/06) and the River Vltava in Prague – Troja

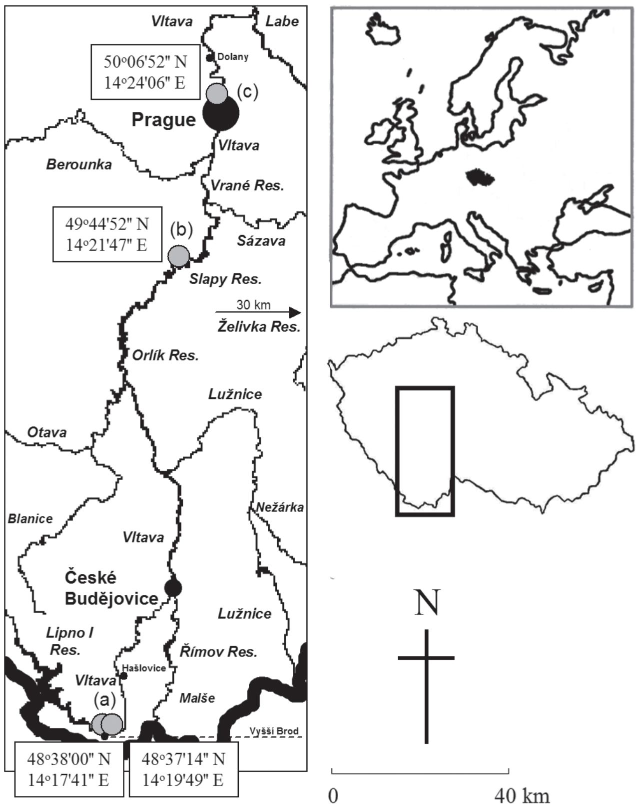

Fig. 1. *A map of the main River Vltava basin, its locations in the Czech Republic and positions of individual roosting places (grey dots) of great cormorant (*Phalacrocorax carbo*) where regurgitated pellets, fish bones and sporadic fish remains were collected (a), (b) or where birds were shot (c). Latitude and longitude is given for each roosting place. (a) the River Vltava in Vyšší Brod (roosting place at Lipno II Reservoir and at the River Vltava); (b) Slapy Reservoir; (c) the River Vltava in Prague – Troja.*

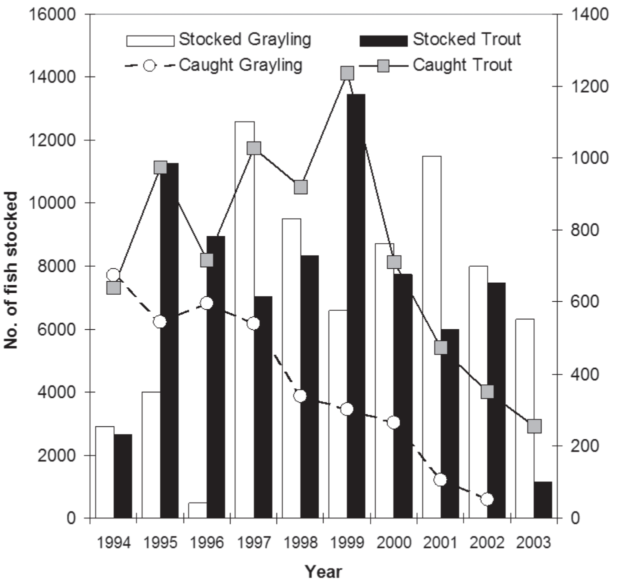

***Fig. 2.** An example of stocking and catch statistics of grayling (*Thymallus thymallus*) and brown trout (*Salmo trutta *m.* fario*) at one of the best trout fisheries in the Czech Republic – Vltava 28 (Czech Anglers Union, unpubl. data), where heavy predation by overwintering great cormorants on fish stock has occurred since mid 90s. Note that in 2003 fishing for grayling was completely prohibited in this fishery.*

(*c*. 45 r. km; winter 2006/07 and 2007/08) (Fig. 1).

At Vyšší Brod, the great cormorants roost on one large spruce (*Picea abies*) at Lipno II Reservoir (area 47 ha, length 2 km, mean and maximum depth 3.6 m and 9 m, volume 1.7 × 10^6 m^3, meso- to eutrophic, 190 km south of Prague) and on spruces and pines (*Pinus sylvestris*) near the River Vltava (mean river depth 0.9 m) approximately 3 km further downstream (on average 73 birds per winter 2004/05, M. Čech, M. Hladík, unpublished data). Lipno II Reservoir serves to regulate water level fluctuations when the hydropower station of Lipno I Reservoir is in operation. Consequently, ice coverage of the reservoir itself and of the river further downstream is very rare. The potential fishing habitat for great cormorants at the River Vltava in Vyšší Brod was Lipno II Reservoir (fishery Vltava 29) and two other river fisheries – Vltava 28 (area 29 ha) and Vltava 27 (area 40 ha) down to the Hašlovice, 15 km north of the roosting colony. Birds have never been observed fishing upstream of the Lipno II Reservoir in the shallow, fast flowing river (M. Hladík, K. Křivanec, pers. comm.). Due to a relatively high altitude (> 500 m a.s.l.) and "normal" winter conditions (mean ± S.D. air temperature –1.3 ± 5.5 °C; Czech Hydrometeorological Institute, unpublished data) other fishing localities, especially ponds and the large Lipno I Reservoir (area 4820 ha, altitude 726 m a.s.l.) were covered by ice for the whole winter, i.e. fish were not accessible to cormorants from these localities.

At Slapy Reservoir (area 1392 ha, length 42 km, mean and maximum depth 19.3 m and 58 m, volume 269 × 10^6 m^3, meso- to eutrophic, 40 km south of Prague), great cormorants roost on pines and oaks (*Quercus robur*) on a steep bank below the Vymyšlenská pěšina natural reserve (on average 60 birds per winter 2005/06, Čech et al. 2008). For most of the winter, the reservoir is filled with relatively warm, hypolimnetic water (7.7-8.5 °C; Čech et al. 2007) 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 & Straškraba 1966), even in severe winters (winter 2005/06 lasted for 4.5 months; mean ± S.D. air temperature –2.5 ± 4.3 °C; Czech Hydrometeorological Institute, unpubl. data) the reservoir is covered by ice for less than two weeks. Since all other water bodies near to Slapy Reservoir were covered by ice for the whole winter of 2005/06 the great cormorants were forced to forage exclusively on this reservoir.

On the River Vltava in Prague – Troja (mean river depth 1.8 m, eu- to hypertrophic), great cormorants roost on poplars (*Populus tremula*) in close proximity to the sewerage plant. Extremely warm weather during the winter of 2006/07 (the warmest winter since year 1922; Czech Hydrometeorological Institute, unpublished data) and very similar weather during the winter of 2007/08 (mean ± S.D. air temperature 6.6 ± 1.8 °C in winter 2006/07 and 4.2 ± 2.5 °C in winter 2007/08) prevented ice covering the River Vltava in Prague and enabled roosting and foraging of over 1000 great cormorants there (P. Musil, pers. comm. and unpublished data). For the purpose of this study, great cormorants roosting on the River Vltava in Prague – Troja were considered to be foraging on the fisheries Vltava 3-7 (528 ha), i.e. from the dam of Vrané Reservoir, 20 km south of the roosting colony, to the weir at Dolany 15 km north of the roosting colony. Due to the lack of valuable telemetric data, however, foraging on other localities further upstream or further downstream could not be completely excluded (Š. Rusňák, J. Andreska, pers. comm.).

Material and Methods

The species composition and sizes of fish prey in the diet of great cormorants were investigated from regurgitated pellets, individual bones and sporadic fish remains collected below the roosting trees on 1 and 21 January, 4 February and on 1 April 2005 (the River Vltava in Vyšší Brod) and on 8 April 2006 (Slapy Reservoir). In detail, *c*. 100 m^2 of the ground was searched each time in the case of the River Vltava in Vyšší Brod, and *c*. 250 m^2 at Slapy Reservoir, from which 1150 ml and 2000 ml of food remains, respectively, were collected. Whole regurgitated material was immersed for one week in concentrated detergent solution, then washed through a sieve (mesh size 1 mm), dried at room temperature and analyzed under a binocular magnifying glass (magnification 8 times and 16 times).

Similar to the findings of Carss et al. (1997) and Čech et al. (2008) at both roosts studied (the River Vltava in Vyšší Brod, Slapy Reservoir), the regurgitated pellets, fish bones and remains are, immediately after the roosting season (frequently even during the roosting season), scavenged by red foxes (*Vulpes vulpes*), feral pigs (*Sus scrofa*) and pine martens (*Martes martes*). Contamination of the samples by regurgitated pellets and fish remains from previous years is therefore negligible.

At the River Vltava in Prague, great cormorants were shot before sunset when arriving at the night roosting trees, i.e. after the second foraging peak of the day, on 27 February (n = 5), 1 March (n = 2), 1 December (n = 8), 2 December (n = 3), 3 December (n = 1), 4 December (n = 1) and 31 December (n = 3) 2007 and on 2 January (n = 1) and 5 January (n = 2) 2008. Permission to shoot was granted by the Department of Nature Conservation of the Prague City Hall. Immediately after the shooting, birds killed were picked up from the water using boats, then measured, weighed and sexed. The stomach and oesophagus were dissected from each bird and deep frozen for later analysis. In the laboratory, analysis of stomach contents was carried out in a similar way to that used for the pellets, since the soft tissues of all fish were at least partly digested (40 % digestion at least; oesophaguses were empty).

To identify the species and sizes of fish preyed upon, a reference collection of diagnostic bones was constructed for each of the potential prey species (see Čech et al. 2008 and this study). For dissection of the bones, fish were taken from gill net and seine net catches from Římov Reservoir and from dip net and fishing rod catches from various streams, rivers and ponds belonging to the River Vltava basin in the years 2000-2008. In total, 254 fish were measured (total length, L_T, to the nearest 0.1 cm), boiled, dissected and the diagnostic bones, selected according to Hallet (1977, 1982), Reynolds & Hinge (1996), Čech & Čech (2006) and Čech et al. (2008), were measured to the nearest 0.1 mm (Fig. 3). Pharyngeal bones (*os pharyngeum*) were selected for cyprinid species (Cyprinidae), lower jaws (*dentale*) for European eel, grayling, trout spp., northern pike (*Esox lucius*) and percid species (Percidae), upper jaws (*maxillare*) for trout spp. and preopercular bones (*praeoperculare*) for bullhead (*Cottus gobio*) and percid species. The measurements selected were the pharyngeal bone tip, PhT, for cyprinid species, dental length, DeL, for European eel, trout spp., northern pike and percid species, maxilar length, MxL, for trout spp., preopercular length, PpL, for bullhead and the preopercular gape, PpG, for percid species (Fig. 3, see also Čech et al. 2008). From the reference material collected, a linear regression equation was established for each of the seven prey species and one hybrid, between the measured dimension of the diagnostic bone and fish total length (Table 1). For the rest of the fish species linear regression equations were taken from the work of Čech et al. (2008; another 357 fish originated from the River Vltava basin dissected for diagnostic bones).

The species-specific identification of salmonid fishes (Salmonidae) is possible only using the praevomer (*praevomer* – a relatively small, fragile bone from the top of the mouth cavity), while the habitus of lower and upper jaws as well as e.g. intermaxilar (*intermaxillare*) and palatal (*palatinum*) bones appear to be the same. Unfortunately, no praevomers were found in the samples, so the category "trout spp." refers to both native brown trout and non-native rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*).

Mass estimates for the fish prey were obtained by using a length-weight regression equation for each fish species from either Želivka Reservoir (Prchalová et al. 2005) or Římov Reservoir and its tributary (J. Kubečka, M. Prchalová, unpublished data), both belonging to the River Vltava basin.

To estimate winter (16 December-15 March) fish withdrawal caused by great cormorants in individual fisheries, the following equation was used: FW = (DFI × N × D) / A where *FW* is the fish withdrawal caused by a roosting colony of great cormorants in the targeted fisheries during the appropriate winter, *DFI* is the daily food intake of individual bird (calculation see below and Fig. 4), *N* is the average number of great cormorants in the roosting colony during the appropriate winter, *D* is the number of foraging

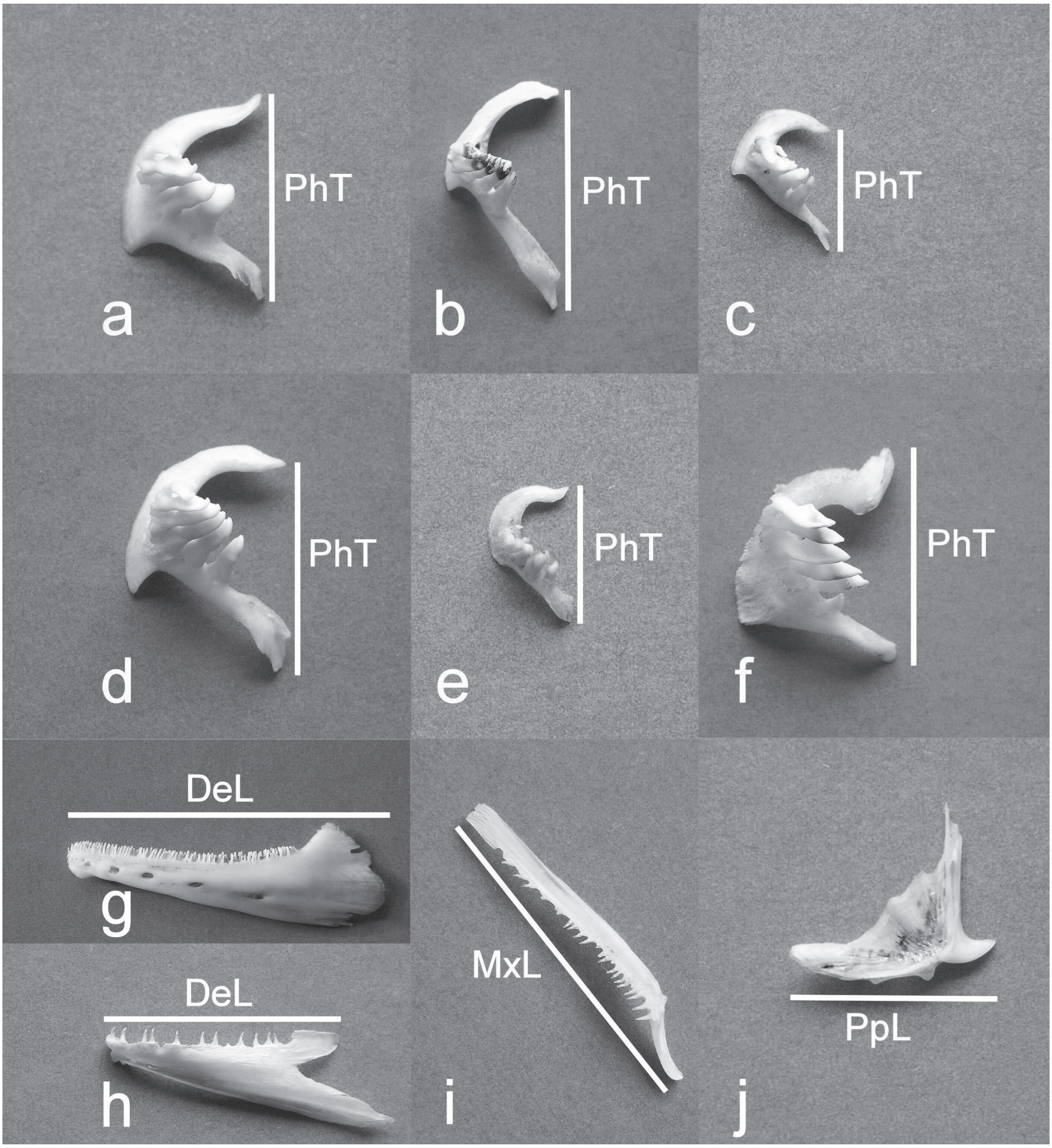

Fig. 3. *Diagnostic bones of selected fish species: pharyngeal bone (os pharyngeum) of (a) roach, (b) bream, (c) common dace, (d) roach × bream hybrid, (e) gudgeon, (f) nase; lower jaw (dentale) of (g) European eel, (h) trout spp.; upper jaw (maxillare) of (i) trout spp.; preopercular bone (praeoperculare) of (j) bullhead. The white line indicates the measurement. PhT, pharyngeal tip; DeL, Dental length; MxL, maxilar length; PpL, preopercular length. Photo M. Čech.*

days (note that $DFI \times N \times D$ is equal to the total fish consumption per roosting colony) and A is the area of potential foraging habitats, i.e. the area of targeted fisheries.

For estimation of the daily food intake (DFI) of great cormorant, the assumption of Carss et al. (1997) that pellets, the stomach contents of shot birds and direct feeding observations cannot be used to derive good estimates of DFI because of the associated biases in estimating diet, was taken into consideration.

Table 1. *Regression equations of total length (L_T; cm) on bone dimensions (mm) for the seven prey fish species and one hybrid. Numbers in parentheses represent the range of fish lengths (cm) from which the equations are derived. PhT, pharyngeal tip; DeL, dental length; MxL, maxilar length; PpL, preopercular length (for details see Fig. 3).*

Species	n	Equation
Roach (*Rutilus rutilus*)	75	L_T = 1.5658PhT + 0.2805 r^2 = 0.9918 (4.1 – 38.0)
Common dace (*Leuciscus leuciscus*)	10	L_T = 1.8579PhT – 0.9119 r^2 = 0.9858 (9.9 – 18.4)
Gudgeon (*Gobio gobio*)	110	L_T = 1.9278PhT – 0.0653 r^2 = 0.9592 (2.8 – 14.0)
Nase (*Chondrostoma nasus*)	7	L_T = 1.4818PhT + 7.5102 r^2 = 0.931 (18.0 – 48.0)
Roach × bream hybrid (*Rutilus rutilus* × *Abramis brama*)	30	L_T = 1.743PhT + 0.943 r^2 = 0.9749 (13.0 – 38.5)
European eel (*Anguilla anguilla*)	10	L_T = 1.7691DeL + 8.800 r^2 = 0.9799 (24.0 – 88.0)
Trout spp.	5	L_T = 1.3191DeL + 2.0274 r^2 = 0.9901 (12.4 – 36.0) L_T = 1.0755MxL + 1.8713 r^2 = 0.9917 (12.4 – 36.0)
Bullhead (*Cottus gobio*)	7	L_T = 1.203PpL – 0.9609 r^2 = 0.9805 (5.4 – 15.0)

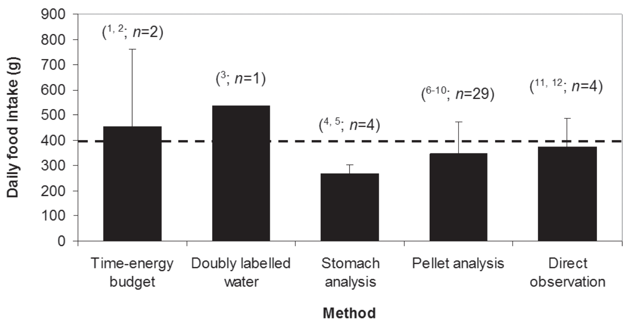

Fig. 4. *Daily food intake (mean + S.D.) of great cormorant (*Phalacrocorax carbo *and* P. c. sinensis*) calculated using different methods according to the work of* [1]*Grémillet et al. (1995),* [2]*Grémillet et al. (2003),* [3]*Keller & Visser (1999),* [4]*Opačak et al. (2004),* [5]*Liordos & Goutner (2007),* [6]*Dirksen et al. (1995),* [7]*Keller (1995),* [8]*Platteeuw & van Eerden (1995),* [9]*Leopold et al. (1998),* [10]*Gagliardi et al. (2007),* [11]*Voslamber et al. (1995),* [12]*Lekuona (2002). Note that values of DFI calculated specifically for the larger, primarily marine subspecies of great cormorant (*P. c. carbo*) were not included. Numbers in parenthesis refer to individual published works (see above), n refers to number of stated values of DFI. Dashed line shows calculated average DFI (397 g), which was used in the present study for the estimate of the total fish consumption in case of the River Vltava in Vyšší Brod, Slapy Reservoir and the River Vltava in Prague.*

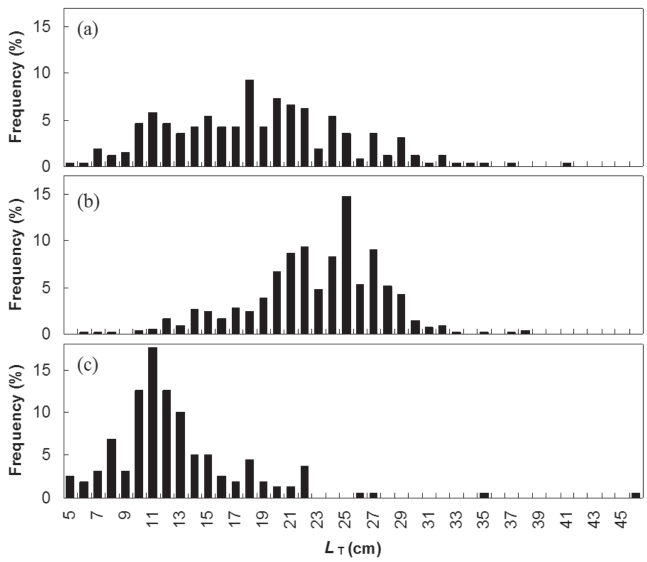

Fig. 5. *Frequency distributions of total length (L_T) of all fish species found in the diets of great cormorants (*Phalacrocorax carbo*) hunting on a) the River Vltava in Vyšší Brod (winter 2004/05; n = 389), b) Slapy Reservoir (winter 2005/06; n = 604) and c) the River Vltava in Prague (winter 2006/07, winter 2007/08, pooled data; n = 159).*

However, calculations of DFI from bioenergetic models and time-energy budgets also include great potential for biases in each step of the calculation

Table 2. *Fish species composition in the diet of great cormorants (*Phalacrocorax carbo*) hunting on the River Vltava in Vyšší Brod, on Slapy Reservoir and on the River Vltava in Prague. Note that in all cases roach was the dominant prey species in terms of weight. n, number of individuals; $\%_a$, percentage of abundance; W, total weight (kg) of all fish of appropriate species caught and digested by great cormorants in the sample; $\%_W$, percentage of total weight. Values of the three most numerous fish species in each individual locality are in bold.*

	Vyšší Brod¶				Slapy Reservoir¶				Prague§							
	winter 04/05				winter 05/06				winter 06/07				winter 07/08			
Species	n	$\%_a$	W	$\%_W$	n	$\%_a$	W	$\%_W$	n	$\%_a$	W	$\%_W$	n	$\%_a$	W	$\%_W$
Roach (*Rutilus rutilus*)	**132**	**33.9**	**16.6**	**41.0**	**502**	**83.1**	**74.2**	**83.4**	**17**	**25.8**	**1.1**	**45.3**	**23**	**24.7**	**0.71**	**29.2**
Bream (*Abramis brama*)	5	1.3	0.9	2.3	1	0.2	0.1	0.1	1	1.5	0.12	4.8	**11**	**11.8**	**0.3**	**12.4**
White bream (*Blicca bjoerkna*)	1	0.3	0.1	0.3	6	1.0	1.1	1.3	-	-	-	-	3	3.2	0.15	6.1
Bleak (*Alburnus alburnus*)	25	6.4	0.3	0.6	5	0.8	0.2	0.2	1	1.5	0.05	2.2	6	6.5	0.19	7.9
European chub (*Squalius cephalus*)	**99**	**25.4**	**10.0**	**24.8**	**18**	**3.0**	**2.9**	**3.3**	4	6.1	0.18	7.4	3	3.2	0.1	4.3
Common dace (*Leuciscus leuciscus*)	4	1.0	0.1	0.3	-	-	-	-	4	6.1	0.09	3.8	4	4.3	0.03	1.2
Gudgeon (*Gobio gobio*)	-	-	-	-	-	-	-	-	**12**	**18.2**	**0.17**	**7.0**	7	7.5	0.07	3.1
Rudd (*Scardinius erythrophthalmus*)	-	-	-	-	2	0.3	0.07	0.07	-	-	-	-	-	-	-	-
Nase (*Chondrostoma nasus*)	-	-	-	-	-	-	-	-	-	-	-	-	1	1.1	0.01	0.5
Tench (*Tinca tinca*)	-	-	-	-	6	1.0	1.0	1.2	-	-	-	-		-	-	-
Common carp (*Cyprinus carpio*)	1	0.3	0.3	0.7	8	1.3	1.3	1.4	-	-	-	-	-	-	-	-
Grass carp (*Ctenopharyngodon idella*)	-	-	-	-	6	1.0	0.5	0.6	-	-	-	-	-	-	-	-
Prussian carp (*Carassius auratus*)†	-	-	-	-	-	-	-	-	1	1.5	0.23	9.6	-	-	-	-
Roach × bream hybrid (*R. rutilus* × *A. brama*)	-	-	-	-	-	-	-	-	-	-	-	-	6	6.5	0.07	3.1
European eel (*Anguilla anguilla*)	-	-	-	-	-	-	-	-	-	-	-	-	1	1.1	0.19	7.7
Grayling (*Thymallus thymallus*)†	1	0.3	0.2	0.4	-	-	-	-	-	-	-	-	-	-	-	-
Trout spp.	3	0.8	0.3	0.8	-	-	-	-	-	-	-	-	-	-	-	-
Northern pike (*Esox lucius*)	2	0.5	0.04	0.09	5	0.8	1.4	1.6	-	-	-	-	1	1.1	0.13	5.2
Bullhead (*Cottus gobio*)	4	1.0	0.01	0.03	-	-	-	-	-	-	-	-	-	-	-	-
European perch (*Perca fluviatilis*)	**96**	**24.7**	**10.6**	**26.2**	**38**	**6.3**	**5.1**	**5.8**	3	4.5	0.22	9.0	3	3.2	0.05	2.2
Ruffe (*Gymnocephalus cernuus*)	14	3.6	0.4	0.9	1	0.2	0.01	0.01	**23**	**34.8**	**0.26**	**10.8**	**24**	**25.8**	**0.42**	**17.2**
Zander (*Sander lucioperca*)	2	0.5	0.7	1.7	6	1.0	0.9	1.0	-	-	-	-	-	-	-	-
Total	389	100	40.5	100	604	100	89.0	100	66	100	2.43	100	93	100	2.41	100

† Species classification and size estimates of one Prussian carp and one grayling was done using own reference collection of diagnostic bones of these species, which originated from ponds, streams and rivers belonging to the River Vltava basin.

¶ Results based on pellets analysis.

§ Results based on stomachs analysis.

(see e.g. Grémillet et al. 1995, Grémillet et al. 2003) and the values of DFI obtained are highly variable (cf. Grémillet et al. 1995 and DFI 238 g day^{-1} for adult *P. carbo sinensis* and Grémillet et al. 2003 and DFI 672 g day^{-1} for adult *P. carbo* – subspecies not stated). The only attempt to calculate DFI of wild great cormorants (*P. c. sinensis*) using a doubly labelled water technique and stable isotopes provides an estimate of DFI of 539 g day^{-1} (Keller & Visser 1999). The main disadvantage of both these methods (time-energy budget, doubly labelled water) is the extremely limited number of birds in the analysis (<< 10 birds). Since all the other methods (pellets and stomachs analysis, direct feeding observations) are often based on hundreds of samples (cf. e.g. Dirksen et al. 1995, Lekuona 2002, Opačak et al. 2004, Gagliardi et al. 2007) for the purpose of this study the DFI was calculated as an average from all the methods mentioned above, i.e. as 397 g day^{-1} (Fig. 4). The data were analyzed using linear regression and one-way ANOVA.

Results

At the River Vltava in Vyšší Brod site during the winter of 2004/05, the regurgitated diet remains of the great cormorants included 389 fish (after pairing the diagnostic bones) of 14 fish species of 5 families (Cyprinidae, Salmonidae, Esocidae, Cottidae, Percidae). Roach (*Rutilus rutilus*), bream (*Abramis brama*), bleak (*Alburnus alburnus*), European chub (*Squalius cephalus*), European perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*) represented 95.3 % (numerically) of the diet (Table 2). From the dominant species, roach taken were in the length range 10-29 cm

Table 3. *Estimated winter fish consumption (total, dominant species – by weight, species of anglers' interest) by great cormorants (*Phalacrocorax carbo*) at the River Vltava in Vyšší Brod, Slapy Reservoir and the River Vltava in Prague. nds, not dominant species, i.e. species presented in the diet but here included in the category "Others". Note that results from Vyšší Brod and Slapy Reservoir are based on pellets analysis while results from Prague are based on stomachs analysis.*

	Vyšší Brod	Slapy Res.	Prague	
	winter 2004/05	winter 2005/06	winter 2006/07	winter 2007/08
Average No. of great cormorants	73*	60†	1000‡	1150‡
No. of foraging days	90	90	90	91
No. of cormorant days	6 570	5 400	90 000	104 650
Daily food intake (g)	397			
Fish consumption – total (kg $winter^{-1}$)	2 608	2 144	35 730	41 546
Area of potential foraging habitats, i.e. area of targeted fisheries (ha)	116	1 392	528	
Fish withdrawal (kg ha^{-1} $winter^{-1}$)	22	2	68	79
Fish of anglers' interest withdrawal (kg ha^{-1} $winter^{-1}$)	1.0	0.07	0	10.2
Consumption of selected species (kg)				
Roach (*Rutilus rutilus*)	**1 069**	**1 788**	**16 186**	**12 131**
Bream (*Abramis brama*)	*nds*	*nds*	*nds*	**5 152**
European chub (*Squalius cephalus*)	**647**	**71**	*nds*	*nds*
Common carp (*Cyprinus carpio*)	18	30	-	-
Grass carp (*Ctenopharyngodon idella*)	-	13	-	-
Prussian carp (*Carassius auratus*)	-	-	**3 430**	-
European eel (*Anguilla anguilla*)	-	-	-	3 199
Grayling (*Thymallus thymallus*)	10	-	-	-
Trout spp.¶	21	-	-	-
Northern pike (*Esox lucius*)	23	34	-	2 160
European perch (*Perca fluviatilis*)	**683**	**124**	*nds*	*nds*
Ruffe (*Gymnocephalus cernuus*)	*nds*	*nds*	**3 859**	**7 146**
Zander (*Sander lucioperca*)	44	21	-	-
Others	91	62	12 255	11 758
Fish of anglers' interest (total)	117	99	0	5 359

** M. Čech, M. Hladík, unpublished data.*
† Čech et al. (2008).
‡ Estimated according to published results of Fišerová & Bergmann (2004), Mourková & Bergmann (2005) and corrected for winter 2006/07 and 2007/08 by P. Musil (unpubl. data and pers. comm.).
*¶ Category "Trout spp." includes both native brown trout (*Salmo trutta *m.* fario*) and non-native rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*).*

(average L_T 21.5 cm), European chub in the length range 7-35 cm (average L_T 18.7 cm) and European perch in the length range 9-37 cm (average L_T 18.4 cm). The largest fish taken by the great cormorants was a 41 cm zander (*Sander lucioperca*), the heaviest was a 734 g European perch (regurgitated prior to complete digestion of the soft tissues). The average size of fish captured and ingested by great cormorants was 18.6 cm L_T and 114 g. Fish ≤ 20 cm L_T comprised 60.3 % of the cormorants' diet at this site (Fig. 5a).

The great cormorants at the River Vltava in Vyšší Brod were estimated to have consumed 2608 kg of fish during the winter of 2004/05 (Table 3). During this period, the estimated roach consumption was 1069 kg, while corresponding values for European perch were 683 kg and for European chub 647 kg. From the fish of interest to anglers, the cormorants consumed 44 kg of zander, 23 kg of northern pike, 21 kg of trout spp., 18 kg of common carp (*Cyprinus carpio*) and 10 kg of grayling. The overall fish withdrawal considering the fisheries Vltava 29 (Lipno II Reservoir), Vltava 28 and Vltava 27 was 22 kg ha^{-1} (Table 3).

In Slapy Reservoir during the winter of 2005/06, the regurgitated diet remains of great cormorants included 604 fish of 13 fish species of 3 families (Cyprinidae, Esocidae, Percidae). Roach, bream, bleak, European chub, European perch and ruffe again represented 93.6 % of the diet (Table 2). From the dominant species, roach in a length range of 6-35 cm (average L_T 22.9 cm), European perch in a range of 11-29 cm (average L_T 21.2 cm) and European chub of 7-31 cm (average L_T 24.3 cm) were taken. The largest fish taken by the great cormorants at this site was a 38 cm northern pike, and the heaviest was a 575 g roach. The average size of fish captured and ingested by great cormorants was 22.8 cm L_T and 157 g. Fish ≤ 20 cm L_T made up only 26.5 % of the cormorants' diet (Fig. 5b).

The great cormorants at Slapy Reservoir were estimated to have consumed 2144 kg of fish during the winter of 2005/06 (Table 3). During this period, estimated roach consumption was 1788 kg, while the corresponding values for European perch were 124 kg and for European chub 71 kg. From the fish of anglers' interest, cormorants consumed 34 kg of northern pike, 30 kg of common carp, 21 kg of zander and 13 kg of grass carp (*Ctenopharyngodon idella*). Thus the overall fish withdrawal when considering the fisheries Vltava 10-14 (Slapy Reservoir) was 2 kg ha^{-1} (Table 3).

On the River Vltava in Prague during the warm winter of 2006/07, the stomachs of seven great cormorants killed included 66 fish of nine species of two families (Cyprinidae, Percidae). Roach, bream, bleak, European chub, European perch and ruffe represented 74.2 % of the diet (Table 2). From these dominant species, ruffe were taken in the length range of 6-12 cm (average L_T 9.2 cm), roach in the range of 8-35 cm (average L_T 15.4 cm) and gudgeon (*Gobio gobio*) 11-14 cm (average L_T 12.6 cm). The largest and heaviest fish taken by the great cormorants at this site was a 35.2 cm and 578 g roach (an exceptional catch by a ringed, large, 5 year old male cormorant of 3700 g net weight). The average size of fish captured and ingested by great cormorants was 13.0 cm L_T and 37 g. Fish ≤ 20 cm L_T comprised 92.4 % of the cormorants' diet. The daily food intake reconstructed from the stomach contents of individual birds was estimated to be 347 ± 193 g of fish (mean ± S.D.; not used for final estimate of total fish consumption).

Great cormorants at the River Vltava in Prague were estimated to have consumed 35730 kg of fish during the winter of 2006/07 (Table 3). During this period, the estimated consumption of roach was 16186 kg, while corresponding values for ruffe were 3859 kg and Prussian carp (*Carassius auratus*) 3430 kg. There were no fish of anglers' interest in the stomachs of great cormorants analysed, but the sample was limited. The overall fish withdrawal considering fisheries Vltava 3-7 was 68 kg ha^{-1} (Table 3).

At the River Vltava in Prague during the warm winter of 2007/08, the stomachs of 19 great cormorants killed included 93 fish of 13 species and 4 families (Cyprinidae, Anguillidae, Esocidae, Percidae). Roach, bream, bleak, European chub, European perch and ruffe represented 75.2 % of the cormorants' diet (Table 2). Of the dominant species, ruffe were taken in the length range 7-13 cm (average L_T 11.1 cm), roach in the range of 5-22 cm (average L_T 12.4 cm), bream in the range of 7-22 cm (average L_T 12.9 cm) and gudgeon 10-14 cm (average L_T 11.3 cm). The largest and heaviest fish taken by the great cormorants was a 46 cm and 185 g European eel. The average size of fish captured and ingested by great cormorants was 12.5 cm L_T and 26 g. Fish ≤ 20 cm L_T comprised 92.5 % of the cormorants' diet at this site. The daily food intake reconstructed from the stomach contents of individual birds was estimated to be 127 ± 129 g of fish (mean ± S.D.). When excluding birds found with empty stomachs ($n = 5$; two males, three females) from the calculation, this weight increased to 173 ± 121 g of fish (mean ± S.D.; not used for final estimate of total fish consumption). Surprisingly low value of DFI was most probably caused by highly turbid, flood water running in the River Vltava on 1-4 December 2007 (13 out of 19 birds shot during these days) causing the visual hunting for fish extremely problematic.

Great cormorants at the River Vltava in Prague were estimated to have consumed 41546 kg of fish during the winter of 2007/08 (Table 3). During this period, estimated consumption of roach was 12131 kg, while corresponding values for ruffe were 7146 kg and bream 5152 kg. From the fish of anglers' interest, cormorants consumed 3199 kg of European eel and 2160 kg of northern pike. The overall fish withdrawal considering the Vltava 3-7 fisheries was 79 kg ha^{-1} (Table 3).

At the River Vltava in Prague, eight fish species – roach, bream, bleak, European chub, common dace (*Leuciscus leuciscus*), gudgeon, European perch and ruffe – were found in the diet of great cormorants during both the 2006/07 and 2007/08 winters. The most hunted fish species was ruffe (made up 34.8 % and 25.8 % of the cormorants' diet in 2006/07 and 2007/08 winters respectively) followed by roach (25.8 % and 24.7 % in the 2006/07 and 2007/08 winters respectively; Table 2). The proportions of roach, bream, bleak, European chub, European perch and ruffe, as well as the proportion of fish ≤ 20 cm L_T, in the diet of great cormorants remained the same in both winters (see above). Similarly, the sizes of fish hunted by the great cormorants in 2006/07 and 2007/08 winters also did not differ significantly (ANOVA: $F_{1, 157} = 0.26$, $P = 0.61$; for pooled data see Fig. 5c).

Discussion

At all three roosting localities on the main stream of the River Vltava, six fish species – roach, bream, bleak, European chub, European perch and ruffe made up at least 74.2 %, i.e. the gross majority, of the cormorants' diet. These results correspond well with most findings throughout large European non-salmonid inland waters (see e.g. Dirksen et al. 1995, Keller 1995, Suter 1997, Keller 1998, Engström 2001, Wziątek et al. 2005, Čech et al. 2008, Fonteneau et al. 2009). Since all these fish species are highly gregarious (Suter 1997, Čech et al. 2005, Čech & Kubečka 2006), moreover, highly abundant in large waters of the Czech Republic, it is not surprising that they form the majority of the diet of piscivorous birds. The similarity of the diets of great cormorants roosting at the River Vltava in Vyšší Bord, Slapy Reservoir and on the River Vltava in Prague (at first sight completely different localities) could be, on the other hand, a great surprise for anglers, since it resembles the diet of cormorants fishing in lakes and reservoirs (for details see references above). However, the River Vltava in Prague is dammed by a series of weirs (six weirs from Vrané Reservoir to the weir in Dolany), and, in reality, this lowland river operates like a cascade of small reservoirs. Similarly, in the case of the River Vltava in Vyšší Brod, there is the small Lipno II Reservoir and another three weirs down to the Hašlovice, giving the river, at least to some extent, reservoir-like characters. From the second view, those stretches of the River Vltava together with Slapy Reservoir are more similar than expected.

The only surprise is the very low presence of trout spp. and grayling in the diet of great cormorants at Vyšší Brod when anglers were certain that the birds are responsible for brown trout and grayling populations being close to collapse and for the significant decrease in their catches. Moreover, Suter (1995) and Keller (1995, 1998) have shown that in cases when salmonids, and especially grayling, are abundant in a river, they are also abundant in the diet of great cormorants. The results of the present study have therefore two possible explanations:

1) The dietary study in Vyšší Brod was commissioned by the Czech Anglers Union – the South Bohemian Board too late, when populations of both native salmonids had already been reduced dramatically. As with roach and the other fish species, grayling is highly gregarious (Suter 1995, Staub et al. 1998) and is, moreover, "stupid fish" (Suter 1997, M. Čech, pers. observation) with very poor avoidance reactions and less tendency to seek shelter. For that reason, this fish species is highly vulnerable to cormorant predation and overwintering great cormorants could easily have decimated the population in the late 90s and at the beginning of the new millennium (i.e. prior to this study). In contrast to grayling, brown trout is a solitary, territorial fish (Sundstrom et al. 2003) with very strong avoidance reactions and a strong tendency to seek shelter. Fishing for hidden brown trout in the cold, fast flowing river must be less profitable for great cormorants (Grémillet et al. 2001). This seems to be the main reason why great cormorants do not fish on the River Vltava upstream of the Lipno II Reservoir (where it is a shallow, fast flowing river; M. Hladík, K. Křivanec, pers. observation). Definitely, fishing for brown trout in a cold, fast flowing river with many boulders/shelters would have a completely different impact on the birds' daily energy requirement than fishing for brown trout in lakes like Loch Leven (Stewart et al. 2005). Therefore, predation pressure by great cormorants has little potential to explain the decrease of brown trout in anglers' catch statistics between the years 1999 and 2003. However, this decrease corresponds well with the decrease in stocking of brown trout in the same years (regression

analysis: $r^2 = 0.80$, $F_{1, 3} = 12.03$, $P < 0.05$; see Fig. 2).
2) Anglers themselves are responsible for the decrease of brown trout and grayling catches. Over the last two decades, the anglers' ability to catch a fish has increased dramatically (new technologies and materials, new know-how from the literature, films and internet). This significant improvement is well documented in the catch statistics of two non-native but heavily stocked salmonid species – rainbow trout and brook trout. For example, the stocking of rainbow trout and brook trout into the fishery Vltava 28 in the years 1994-2003 revealed no trend (regression analysis: $P > 0.65$ for both species; the fish stocking size exceeds the minimum size limit for put and take fishery). However, their catch increased significantly over the years (regression analysis: $r^2 = 0.48$, $F_{1, 8} = 7.26$, $P < 0.05$ for rainbow trout and $r^2 = 0.42$, $F_{1, 8} = 5.73$, $P < 0.05$ for brook trout). Moreover, in the years 1994-2003, the average anglers' yield of all fish species from the fishery Vltava 28 exceeded 60 kg ha^{-1} to which the yield of salmonids contributed over 45 kg ha^{-1} (Czech Anglers Union, unpublished data). On the other hand, in the neighbouring fishery, Vltava 27, the average anglers' yield of all fish species (years 1994-2003) exceeded only 18 kg ha^{-1} to which the yield of salmonids contributed over 13 kg ha^{-1} (Czech Anglers Union, unpublished data).

In accordance with the stocking strategy of the Czech Anglers Union – the South Bohemian Board (M. Hladík, pers. comm.), it could also be possible that anglers fishing on the River Vltava in Vyšší Brod, although they catch all the salmonids, they take only non-native species and selectively release the native brown trout and grayling, especially in a situation when it is generally supposed that populations of those two species are close to collapse. This shift in anglers' behaviour in recent years could have a similar effect on the catch statistics of brown trout and grayling as the predation pressure by great cormorants (biasing the real state of the brown trout and grayling populations). The above mentioned put and take strategy to protect populations of native species, could also have a negative effect, since heavily stocked rainbow trout and brook trout could impose food and space competition on both brown trout and grayling, and cause further decline of their populations (Blanchet et al. 2007, Fausch 2007).

Most likely, the truth will be somewhere between explanations 1 and 2: most probably a cumulative effect of both great cormorants and anglers on the populations of brown trout and grayling, exacerbated by river fragmentation and degradation of spawning and nursery habitats. No doubt, one can also hypothesized that both anglers and cormorants are responding to, rather than being responsible for, changes in fish populations (Davies 1997). Unfortunately, the data to test this assumption are missing in case of targeted study sites. On the other hand, restrictions, which have been applied to Vltava 28 and Vltava 27 fisheries since 2005 (fly-fishing only, barbless hooks, catch and release stretches, minimum size limit for brown trout 45 cm) seem to have led to a noticeable recovery of both brown trout and grayling populations (M. Hladík, pers. comm.). Despite this stock improvement there is still a persistent idea of the need to somehow protect the brood stock of grayling against the overwintering great cormorants. One possibility is to catch most of the adult fish prior to the cormorants' arrival and place them in the store-ponds. A part of this brood stock would be used for artificial spawning and yearling production, and the rest of the adult fish will be restocked into the fishery in the same manner as rainbow trout and brook trout, i.e. after the great cormorants leave the river in mid-March (M. Hladík, pers. comm.).

The present study shows that great cormorants hunting on the main stream of the River Vltava prey mostly on coarse fishes of low or even no- interest to anglers. Therefore, it could be easily concluded that the competition between great cormorants and anglers is of minor importance, which would be consistent with findings of other authors (e.g. Keller 1995, Keller 1998, Engström 2001, Wziątek et al. 2005, Liordos & Goutner 2007). This statement is particularly true in the case of Slapy Reservoir where overall fish withdrawal caused by overwintering great cormorants (2 kg ha^{-1}) is similar to the published withdrawal from Lake Veluwemeer, The Netherlands (2.1 kg ha^{-1}; Dirksen et al. 1995), or Želivka Reservoir, Czech Republic (2 kg ha^{-1} $month^{-1}$; Čech & Čech 2009). The removal of mostly zooplanktivorous fish is considered to have a positive influence on water quality of those large water bodies – the top down effect of great cormorants is a substitute for human biomanipulation interventions into the lake/reservoir ecosystem (Dirksen et al. 1995, Čech & Čech 2009). On the other hand, the estimated withdrawal of 22 kg ha^{-1} of fish from the River Vltava in Vyšší Brod (fishery Vltava 27-29) and of 68-79 kg ha^{-1} from the River Vltava in Prague (fishery Vltava 3-7) belong among the highest ever published figures for withdrawal caused by great cormorants from any inland waters (carp fishponds excluded; cf. Dirksen et al. 1995, Suter 1995, Staub et al. 1998, Engström 2001). Therefore, the potential for competition and conflict with anglers is substantial.

This study also shows a peculiar preference for much smaller fish than expected (cf. Čech et al. 2008) for cormorants hunting on the River Vltava in Prague. This finding has at least two possible explanations:

1) The great cormorants are hunting preferentially in Prague's harbours (e.g. under the Charles Bridge) or below Prague's sewerage plant outlet, where extremely high abundance of these small fish was observed many times (Š. Rusňák, J. Andreska, pers. observation).

2) Another reason could be extremely warm winters (both 2006/07 and 2007/08 winters), which could have changed the daily energy budget of great cormorants significantly (Grémillet et al. 2001). Both alternatives result in a situation where cormorants are not forced by natural conditions to prey on larger fish. It must be also taken into account that results from the River Vltava in Prague are based on stomachs analysis while the results from the River Vltava in Vyšší Brod and Slapy Reservoir as well as published relationships between the size of fish taken by great cormorants and air/water temperature (Čech et al. 2008) are based on pellets analysis. It seems that by using pellets, especially very small fish could be to some extent underestimated in the diet of great cormorants (Carss et al. 1997).

Acknowledgement

The authors thank M. Hladík and P. Čech for help with data collection at the River Vltava in Vyšší Brod (MH) and Slapy Reservoir (PČ), J. Andreska for shooting the birds in Prague – Troja, experts from the Prague Zoo for dissecting the birds and all the biometric measurements and Š. Rusňák for providing the stomachs of 26 killed birds and for the initiation of the study in Prague. M. Hladík, the head manager of the fish stocking program of the Czech Anglers Union – the South Bohemian Board, provided the long term data on stocking and catch statistics as well as valuable comments to the situation at the River Vltava in Vyšší Brod. M. Morris carefully read the latest version of the manuscript and corrected the English. The study was supported by the Grant Agency of the Czech Republic (projects No. 206/06/1371 and 206/09/P266), the Academy of Sciences of the Czech Republic (projects No. 1QS600170504 and AVOZ60170517), the Czech Anglers Union – the South Bohemian Board and Š. Rusňák. The paper is dedicated to the boss of the Fish Ecology Unit (FishEcU), J. Kubečka, to his 50th birthday.

Literature

Barrett R.T., Røv N., Loen J. & Montevecchi W.A. 1990: Diets of shags *Phalacrocorax aristotelis* and cormorants *P. carbo* in Norway and possible implications for gadoid stock recruitment. *Mar. Ecol. – Prog. Ser. 66: 205–218.*

Blanchet S., Loot G., Grenouillet G. & Brosse S. 2007: Competitive interactions between native and exotic salmonids: a combined field and laboratory demonstration. *Ecol. Freshw. Fish 16/2: 133–143.*

Carss D.N. & Ekins G.R. 2002: Further European integration: mixed sub-species colonies of great cormorants *Phalacrocorax carbo* in Britain – colony establishment, diet, and implications for fisheries management. *Ardea 90: 23–41.*

Carss D.N., Bevan R.M., Bonetti A., Cherubini G., Davies J., Doherty D., El Hili A., Feltham M.J., Grade N., Granadeiro J.P., Grémillet D., Gromadzka J., Harari Y.N.R.A., Holden T., Keller T., Lariccia G., Mantovani R., McCarthy T.K., Mellin M., Menke T., Mirowska-Ibron I., Muller W., Musil P., Nazirides T., Suter W., Trauttmansdorff J.F.G., Wilhelminenberg O., Volponi S. & Wilson B. 1997: Techniques for assessing cormorant diet and food intake: towards a consensus view. *Supplementi di Ricerche Biologia Selvaggina 26: 197–230.*

Čech M. 2004: The diet of great cormorant on reservoirs. *Rybářství 2: 14–15. (in Czech)*

Čech M. & Čech P. 2006: Diet of kingfisher at various types of waters. In: Čech P. (ed.), Proceedings of 1th international kingfisher (*Alcedo atthis*) seminar. *Czech Union for Nature Conservation, Vlašim, Czech Republic: 55–71. (in Czech with extended abstract in English)*

Čech M. & Čech P. 2009: The diet of great cormorants (*Phalacrocorax carbo*) at Želivka water supply reservoir. *Sborník vlastivědných prací z Podblanicka 48: 91–105. (in Czech with English summary)*

Čech M. & Kubečka J. 2006: Ontogenetic changes in the bathypelagic distribution of European perch fry *Perca fluviatilis* monitored by hydroacoustic methods. *Biologia 61: 211–219.*

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.*

Čech M., Kratochvíl M., Kubečka J., Draštík V. & Matěna J. 2005: Diel vertical migrations of bathypelagic perch fry. *J. Fish Biol. 66: 685–702.*

Čech M., Kubečka J., Frouzová J., Draštík V., Kratochvíl M., Matěna J. & Hejzlar J. 2007: Distribution of the

bathypelagic perch fry layer along the longitudinal profile of two large canyon-shaped reservoirs. *J. Fish Biol. 70: 141–154.*
Davies J.M. 1997: Impacts of cormorants (*Phalacrocorax carbo* L.) on the Lower River Ribble Fishery, Lancashire. *Ph.D. thesis, Liverpool John Moores University, United Kingdom.*
Dirksen S., Boudewijn T.J., Noordhuis R. & Marteijn E.C.L. 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: 167–184.*
Engström H. 2001: Long term effects of cormorant predation on fish communities and fishery in a freshwater lake. *Ecography 24: 127–138.*
Fausch K.D. 2007: Introduction, establishment and effects of non-native salmonids: considering the risk of rainbow trout invasion in the United Kingdom. *J. Fish Biol. 71: 1–32.*
Fonteneau F., Paillisson J.-M. & Marion L. 2009: Relationships between bird morphology and prey selection in two sympatric great cormorant *Phalacrocorax carbo* subspecies during winter. *Ibis 151: 286–298.*
Gagliardi A., Martinoli A., Preatoni D., Wauters L.A. & Tosi G. 2007: From mass of body elements to fish biomass: a direct method to quantify food intake of fish eating birds. *Hydrobiologia 583: 213–222.*
Grémillet D. 1997: Catch per unit effort, foraging efficiency, and parental investment in breeding great cormorants (*Phalacrocorax carbo carbo*). *ICES J. Mar. Sci. 54: 635–644.*
Grémillet D., Schmid D. & Culik B. 1995: Energy requirements of breeding great cormorants *Phalacrocorax carbo sinensis*. *Mar. Ecol. – Prog. Ser. 121: 1–9.*
Grémillet D., Wanless S., Carss D.N., Linton D., Harris M.P., Speakman J.R. & Le Macho Y. 2001: Foraging energetics of Arctic cormorants and the evolution of diving birds. *Ecol. Lett. 4: 180–184.*
Grémillet D., Wright G., Lauder A., Carss D.N. & Wanless S. 2003: Modelling the daily food requirements of wintering great cormorants: a bioenergetics tool for wildlife management. *J. Appl. Ecol. 40: 266–277.*
Hallet C. 1977: Contribution a l´étude du régime alimentaire du Martin-pêcheur (*Alcedo atthis*) dans la vallée de la Lesse. *Aves 14: 128–144.*
Hallet C. 1982: Etude du comportement de predation du Martin-pêcheur *Alcedo atthis* (L.): taille preferentielle de capture du Chabot *Cottus gobio* L. et de la Truite *Salmo trutta* L. *Rev. Ecol. (Terre Vie) 36: 211–222.*
Hrbáček J. & Straškraba M. 1966: Horizontal and vertical distribution of temperature, oxygen, pH and water movement in Slapy Reservoir (1958-1960). In: Hrbáček J. (ed.), Hydrobiological studies 1. *Academia Publishing House of the Czechoslovak Academy of Sciences, Prague: 7–40.*
Johansen R., Pedersen T. & Barrett R.T. 1999: Cormorants (*Phalacrocorax carbo carbo*) as predators in a cod (*Gadus morhua* L.) enhancement area in north Norway. In: Howell B., Moksness E. & Svåsand T. (eds.), Stock enhancement and sea ranching. *Fishing News Books, Oxford: 334–349.*
Keller T. 1995: Food of cormorants *Phalacrocorax carbo sinensis* wintering in Bavaria, southern Germany. *Ardea 83: 185–192.*
Keller T. 1998: The food of cormorants (*Phalacrocorax carbo sinensis*) in Bavaria. *J. Ornithol. 139: 389–400.*
Keller T.M. & Visser G.H. 1999: Daily energy expenditure of great cormorants *Phalacrocorax carbo sinensis* wintering at Lake Chiemsee, southern Germany. *Ardea 87: 61–69.*
Lekuona J.M. 2002: Food intake, feeding behaviour and stock losses of cormorants, *Phalacrocorax carbo*, and grey herons, *Ardea cinerea*, at a fish farm in Arcachon Bay (southwest France) during breeding and non-breeding season. *Folia Zool. 51: 23–34.*
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 Dutch Wadden Sea. *J. Sea Res. 40: 93–107.*
Lilliendahl K. & Solmundsson J. 2006: Feeding ecology of sympatric European shag *Phalacrocorax aristotelis* and great cormorants *P. carbo* in Iceland. *Mar. Biol. 149: 979–990.*
Liordos V. & Goutner V. 2007: Spatial patterns of winter diet of the great cormorant in coastal wetlands of Greece. *Waterbirds 30: 103–111.*
Liordos V. & Goutner V. 2008: Habitat and temporal variation in the diet of great cormorant nestlings in Greek colonies. *Waterbirds 31: 424–437.*
Mourková J. & Bergmann P. 2005: Winter waterfowl census in central Bohemia in winter 2003/2004. *Zprávy ČSO 60: 5–18. (in Czech with English summary)*
Mous P.J. 2000: Interactions between fisheries and birds in Ijsselmeer, the Netherlands. *Ph.D. thesis, Wageningen*

University, The Netherlands.
Opačak A., Florijančić T., Horvat D., Ozimec S. & Bodakoš D. 2004: Diet spectrum of great cormorants (*Phalacrocorax carbo sinensis* L.) at the Donji Miholjac carp fishponds in eastern Croatia. *Eur. J. Wildlife Res. 50: 173–178.*
Platteeuw M. & van Eerden M. 1995: Time and energy constraints of fishing behaviour in breeding cormorants *Phalacrocorax carbo sinensis* at Lake Ijsselmeer, The Netherlands. *Ardea 83: 223–234.*
Prchalová M., Kubečka J., Jůza T., Říha M., Jarolím O. & Tušer M. 2005: Complex fish stock assessment of Želivka Reservoir in year 2004. *Report of the Hydrobiological Institute, Academy of Sciences of the Czech Republic: 1–22. (in Czech)*
Reynolds S.J. & Hinge M.D.C. 1996: Foods brought to the nest by breeding kingfisher *Alcedo atthis* in the New Forest of southern England. *Bird Study 43: 96–102.*
Staub E., Egloff K., Krämer A. & Walter J. 1998: The effect of predation by wintering cormorants *Phalacrocorax carbo* on grayling *Thymallus thymallus* and trout (Salmonidae) populations: two case studies from Swiss rivers. Comment. *J. Appl. Ecol. 35: 607–610.*
Stewart D.C., Middlemas S.J., Gardiner W.R., Mackay S. & Armstrong J.D. 2005: Diet and prey selection of cormorants (*Phalacrocorax carbo*) at Loch Leven, a major stocked trout fishery. *J. Zool. 267: 191–201.*
Sundstrom L.F., Lohmus M. & Johnsson J.I. 2003: Investment in territorial defence depends on rearing environment in brown trout (*Salmo trutta*). *Behav. Ecol. Sociobiol. 54: 249–255.*
Suter W. 1995: The effect of predation by wintering cormorants *Phalacrocorax carbo* on grayling *Thymallus thymallus* and trout (Salmonidae) populations: two case studies from Swiss rivers. *J. Appl. Ecol. 32: 29–46.*
Suter W. 1997: Roach rules: shoaling fish are a constant factor in the diet of cormorants *Phalacrocorax carbo* in Switzerland. *Ardea 85: 9–27.*
Suter W. 1998: The effect of predation by wintering cormorants *Phalacrocorax carbo* on grayling *Thymallus thymallus* and trout (Salmonidae) populations: two case studies from Swiss rivers. Reply. *J. Appl. Ecol. 35: 611–616.*
Veldkamp R. 1995: Diet of cormorants *Phalacrocorax carbo sinensis* at Wanneperveen, The Netherlands, with special reference to bream *Abramis brama*. *Ardea 83: 143–155.*
Voslamber B., Platteeuw M. & van Eerden M. 1995: Solitary foraging in sand pits by breeding cormorants *Phalacrocorax carbo sinensis*: does specialized knowledge about fishing sites and fish behaviour pay off? *Ardea 83: 213–222.*
Wziątek B., Martyniak A., Hliwa P., Kozłowski J., Krzywosz T., Osewski M., Sobocki M., Szymańska U. & Gomułka P. 2005: Great cormorant predation on coregonid fishes at seven sites in Poland. *Advanced Limnology – Biology and Management of Coregonid Fishes 60: 285–297.*