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Authors: Emmrich, Matthias, and Düttmann, Heinz

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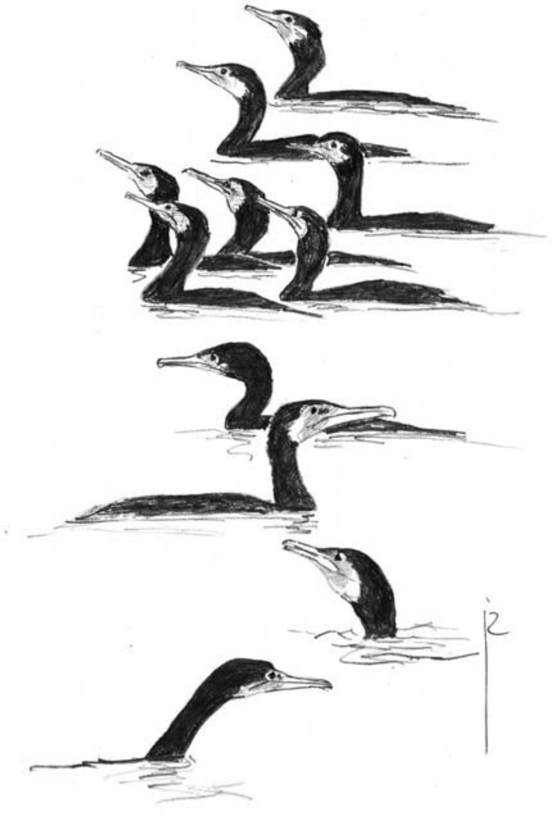
Seasonal shifts in diet composition of Great Cormorants *Phalacrocorax carbo sinensis* foraging at a shallow eutrophic inland lake

Matthias Emmrich[1,*] **& Heinz Düttmann**[2]



Emmrich M. & Düttmann H. 2011. Seasonal shifts in diet composition of Great Cormorants *Phalacrocorax carbo sinensis* foraging at a shallow eutrophic inland lake. Ardea 99: 207–216.

The diet of Great Cormorants *Phalacrocorax carbo sinensis* at Lake Dümmer, a shallow eutrophic lake of 1240 ha in Lower Saxony (Germany) was analysed by collecting 562 regurgitated pellets over a period of one year. Pellets contained structures of 10,645 fishes belonging to 15 species. Substantial differences were found in frequency, composition and size of prey fish species. Pikeperch, Ruffe, Roach and Perch accounted for the largest seasonal differences in the diet. During late autumn and winter the diet was dominated by small-sized cyprinids and Ruffe. In spring Great Cormorants primarily foraged on larger-sized cyprinids. Young-of-the-year percids, dominated by Pikeperch, were the primary prey during summer. We estimated that at least 32.6 tons (26.3 kg/ha) of total fish biomass was removed by Cormorants, of which one third (10.8 tons) consisted of Pikeperch. 81% of the Pikeperch biomass was removed in August–September, indicating that the Great Cormorant is an important predator of juvenile Pikeperch at Lake Dümmer. Our findings highlight the need of extensive diet analyses in all seasons to obtain a comprehensive picture of the impact of Cormorant predation on fish stocks. Snapshots of the diet sampled over short-time periods may be misleading and inadequate for local management.

Key words: pellet analysis, YOY fish, prey shifting, Pikeperch, Cormorant predation, biomass removal

[1]Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Department of Biology and Ecology of Fishes, Müggelseedamm 310, D-12587 Berlin, Germany; [2]Am Bleissmer 25, 31683 Obernkirchen, Germany;
*corresponding author (emmrich@igb-berlin.de)

Of the two subspecies of Great Cormorants *Phalacrocorax carbo* occurring in Europe, the continental *P. c. sinensis* has rapidly increased in breeding numbers in almost all countries over the last decades (Lindell *et al.* 1995, Bregnballe *et al.* 2003). This increase was accompanied by an expansion of geographical range resulting in a re-colonization of areas after a long absence, as well as colonization of previously unoccupied waters. This increase was due to Great Cormorants having benefited from the protective EEC-Directive 79/409 on the Conservation of Wild Birds in the European Union, in combination with an abundant food supply. Eutrophication of inland waters resulted in an increase in fish numbers and biomass, thus favouring the foraging conditions for this opportunistic piscivore (de Nie 1995, van Eerden *et al.* 1995).

The abundant presence of Cormorants has provoked widespread conflicts between stakeholders of nature conservation and fisheries interests (Duffy 1995, Cowx 2003, Behrens *et al.* 2008). Some studies have indicated that Cormorants reduced endangered fish populations or caused economic damage to inland fisheries (Kennedy & Greer 1988, Schenk 1997, Lekuona 2002, Winfield *et al.* 2002, Stewart *et al.* 2005), whereas others observed little impact on fish stocks (Keller 1995, Engström 2001, Martyniak *et al.* 2003, Liordos & Goutner 2007, Boström *et al.* 2009). There has been particular emphasis on using diet analysis to assess the impact of Cormorant predation on freshwater fish stocks (e.g. van Dobben 1952, Kennedy & Greer 1988, Engström 2001, Boström *et al.* 2009). These studies demonstrate that Cormorants have a very varied diet, highlighting the need for site-specific studies to investigate local impacts of Cormorant predation on fish stocks (Winfield *et al.* 2002, Russel *et al.* 2003).

Cormorants are highly opportunistic feeders and prey availability is the most important factor determining their diet (Richner 1995, Carpentier *et al.* 2003, Santoul *et al.* 2004). Fish community structure can vary over time, potentially leading to shifts in the diet of Cormorants. For example, in the Gulf of Finland, Lehikoinen (2005) observed prey shifts in Cormorants during the breeding season. Similarly, seasonal variations in diet composition were found at the Vistula Lagoon (Poland) and the river Garonne (France) (Martyniak *et al.* 2003, Santoul *et al.* 2004). These authors investigated prey availability in coastal or fluvial ecosystems, which may be more variable compared to some inland lakes because of higher proportions of seasonally migrating fish (Lucas & Baras 2001). Furthermore, water temperature and fish recruitment influence the prey choice of Cormorants, with larger fishes taken at lower water temperatures and smaller fishes primarily taken when abundance of young-of-the-year (YOY) fishes is highest (Čech *et al.* 2008, Wolter & Pawlizki 2003).

In the present study, we investigated prey selection of Great Cormorants at Lake Dümmer, a shallow eutrophic lake in western Lower Saxony (Germany). We collected regurgitated pellets over a period of one year to address the following questions. (1) Do Great Cormorants show seasonal changes in composition and size of prey fishes at Lake Dümmer, and what are the preferred species and size classes in different seasons? (2) How extensive is the removal of fish biomass by Great Cormorants in the course of a year?

METHODS

Study area

Lake Dümmer (1240 ha, 52°31'N, 8°20'E) is a shallow, polymictic lowland lake with a mean depth of 1.1 m, and a maximum depth of 4 m (Fig. 1). Water quality deteriorated rapidly following the construction of an embankment in 1953 that resulted in nutrient accumulation, primarily caused by inflow from a small tributary with an agriculture dominated catchment area (Kämmereit *et al.* 2005). The formerly extensive submersed flora disappeared, while heavy blue-green algae blooms started to occur during spring and summer. Currently, large beds of water lilies Nymphaeaceae are found in the littoral zones. Sixteen fish species and one cyprinid hybrid form were detected in Lake Dümmer within the study period and catches from multi-mesh gillnets set in August 2007 were numerically dominated by Roach *Rutilus rutilus* (40.3%), Bream *Abramis brama* (26.9%), Pikeperch *Sander lucioperca* (10.2%), Ruffe *Gymnocephalus cernuus* (9.9%) and White Bream *Blicca bjoerkna* (4.4%). All other species were of minor importance (<4.0%; M. Kämmereit, unpubl. data). Lake Dümmer is used for recreational and commercial fisheries. Declining fish catches for commercially important Eel *Anguilla anguilla*, Pikeperch, Perch *Perca fluviatilis* and Pike *Esox lucius* were linked to increasing numbers of Cormorants (Kämmereit *et al.* 2005). Today, commercial gill-net fishing on Pike, Perch and Pikeperch is almost completely closed and only fyke-net fishing targeting Eel still occurs (L. Dobberschütz, pers. comm.).

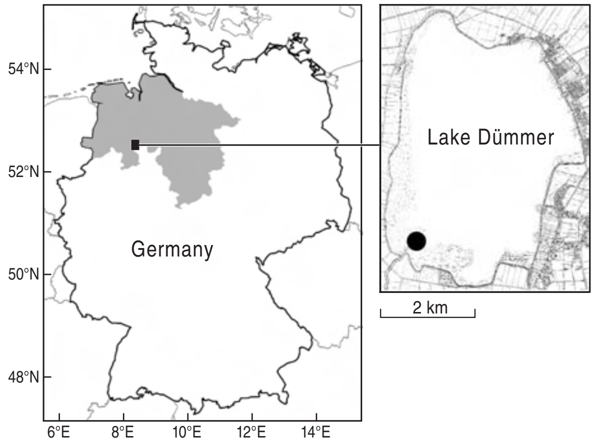


Figure 1. Location of Lake Dümmer in Lower Saxony (shaded area), Germany. The black circle indicates the position of the main roosting trees of Great Cormorants and the location of pellet collection.

Numbers of Great Cormorants at Lake Dümmer have increased from only a few birds in the 1960s (Ludwig *et al.* 1990) to more than 1300 in recent times, with a yearly average of 70,000 cormorant-days (maximum 127,000) (Kämmereit *et al.* 2005). Between-month variability is high but follows a general pattern. Increasing bird numbers are observed in the course of summer, with peaks in September and October. In winter and spring Cormorant numbers are usually decreasing, but may vary considerably due to weather conditions. The lowest numbers of Great Cormorants occur in May and June, when only a few immatures, adults and the breeding pairs are present. Great Cormorants use Lake Dümmer for roosting and foraging and only a few birds forage on other waters in adjacent areas. Consequently, pellets collected at the main roost site should primarily reflect the presence and availability of prey fishes in Lake Dümmer.

Pellet analysis

Pellets were collected during 29 days between October 2007 and September 2008 under the main roosting trees (Fig. 1). Cormorants produce in general one pellet per day and each pellet contains the fish remains of the diet from the previous day (Zijlstra & van Eerden 1995). Whenever possible, samples of Cormorant pellets were collected weekly or biweekly. Only fresh, mucus-coated complete pellets were collected and stored at –18°C. Pellets were soaked in warm water and all relevant diagnostic hard structures from the prey fishes (otoliths, pharyngeal bones, operculae, preoperculae, jaws) were collected and air-dried. Recovery rates of hard structures can vary substantially depending on fish species and size (Zijlstra & van Eerden 1995). The maximum number of prey items per pellet was defined as the highest total of hard structures present, taking right and left parts separately. Corrections were made if fish structures obviously belonged to different individuals, e.g. based on differences in size. Identification of prey fishes was primarily carried out via species-specific otolith characteristics using a reference collection. Otoliths of cyprinids without such characteristics were grouped as cyprinids, or in the case of small Pikeperch or Perch otoliths as percids. Whenever present, small individuals were identified by pharyngeal bones or jaws to species level. For estimation of prey size all key structures were measured either by viewing under a binocular microscope (otoliths <5 mm) or by using callipers (larger structures ≥5mm). In all cases measurements were made with an accuracy of 0.1 mm.

Estimate of fish size

Between April and September 2008 we collected individuals of the most frequent fish species in Lake Dümmer from fyke-net catches (Appendix 1). We calculated species-specific length–weight relationships following the equation $W = a \times TL^b$ by recording total length (TL) and wet biomass (W) of these individuals (accuracy 0.1 cm for TL and 0.1 g for W). After boiling the skulls, relevant hard structures (sagittal otoliths, pharyngeal bones, operculae, preoperculae, jaws) were dissected and subsequently air-dried for at least three days. To estimate prey-fish length from the hard structures we used linear regressions (Appendix 1). In the case of Eel and Pike we used regression formulae from literature (Dirksen *et al.* 1995) because we did not have sufficient reference fishes. Biomass of unidentifiable cyprinids was estimated using the regression models for Roach, Bream and White Bream according to their proportions in the catches of multi-mesh gillnets in 2007, when 92% of all small cyprinids (≤15 cm) belonged to these three species.

Young-of-the-year fishes (YOY)

Based on the maximum TL at age one and Bertalanffy growth models, we estimated the proportion of YOY fishes of the cyprinids Roach, Bream and White Bream in the Cormorants' diet (J. Ludwig, unpubl. data). For the percids Perch, Ruffe and Pikeperch we calculated the overall proportion of YOY fishes in the diet by determining maximum length of approximately one year old individuals from fish catches in spring 2008.

Estimate of biomass removal

Total fish consumption per species was calculated by multiplying monthly averages of the number of cormorant-days by the Daily Food Intake (DFI) and the biomass proportion of the species in the pellets. DFI was based on the estimate of fish biomass from the pellets. Data on cormorant-days were provided by Naturschutzring Dümmer, who counted Great Cormorants in a standardized way at their roosts and breeding grounds. Counts were performed weekly in autumn and winter and at least monthly during spring and summer.

Statistical analyses

Monthly differences in estimated prey biomass, prey frequency, proportion of YOY and of large fishes (≥20 cm) were tested using non-parametric Kruskal Wallis ANOVA which, when significant, was followed by Bonferroni-adjusted Mann–Whitney U tests. Correspondence analysis (CA) was used to illustrate monthly differences in the composition of prey species. In addition, we compared the relative abundance of fish species in the pellets between seasons using multivariate analysis of similarity (ANOSIM, Bray–Curtis distance, 9999 permutations). Fish species that contributed most to seasonal differences were subsequently determined by SIMPER (similarity percentages) analysis. Species with only one individual present in the pellets were excluded from the analyses. Statistical analyses were performed using R (version 2.6.2, R Development Core Team 2008) including the package 'ca' (version 0.2.1, 2007). ANOSIM and SIMPER were calculated using PAST (Hammer *et al.* 2001) version 2.04.

RESULTS

In total, we collected 562 pellets on 29 sampling days (on average 50 pellets per month). Average number of pellets was highest in 2007 ($n = 80$; four sampling days per month), slightly lower in winter and spring 2008 ($n = 66$ and 51; two or three sampling days per month) and lowest in summer 2008 ($n = 22$, one or two sampling days per month). In 30 pellets we found no fish remains at all and these were excluded from analyses.

We found hard structures of 10,645 prey fishes belonging to 15 species. Ruffe, Perch, Roach, Bream, White Bream and Pike were found on over 20 of the 29 sampling dates, while all other species occurred less often (Table 1). Non-identified cyprinids, Ruffe, Pikeperch, Perch and Roach were most numerous in the Cormorants' diet (Table 1). The most numerous species also contributed most to digested biomass, but the order of importance differed; e.g. Roach biomass was three times higher than its frequency (Table 1).

Frequency of prey fishes

The number of fishes per pellet ranged from 1 to 114 with significant differences between months (Kruskal–Wallis $\chi^2 = 72.8$, $df = 10$, $P < 0.001$). Post-hoc tests showed significantly higher numbers of prey per pellet in summer (July–September) compared to the rest of the year ($P < 0.01$; Fig. 2A).

Table 1. Frequency of occurrence, percentages of numbers and of biomass of fish taxa in pellet samples of Great Cormorants at Lake Dümmer collected between October 2007 and September 2008 ($n = 562$).

Species	Frequency of occurrence (%)	Percentage by numbers	Percentage by biomass
Ruffe *Gymnocephalus cernuus*	100.0	28.29	15.36
Perch *Perca fluviatilis*	100.0	8.78	13.76
Cyprinids	96.6	31.49	7.18
Roach *Rutilus rutilus*	90.0	8.23	27.79
Bream *Abramis brama*	86.2	1.22	2.87
White Bream *Blicca bjoerkna*	79.3	1.47	6.89
Pike *Esox lucius*	75.9	0.62	1.72
Pikeperch *Sander lucioperca*	65.5	15.89	16.56
Bleak *Alburnus alburnus*	48.3	0.28	0.64
Eel *Anguilla anguilla*	41.4	0.20	3.13
Ide *Leuciscus idus*	34.5	0.12	0.67
Percids	17.2	3.17	2.06
Rudd *Scardinius erythrophthalmus*	17.2	0.12	0.84
Tench *Tinca tinca*	17.2	0.08	0.49
Carassius sp.	3.4	0.01	0.01
Gudgeon *Gobio gobio*	3.4	0.01	0.01
Dace *Leuciscus leuciscus*	3.4	0.01	0.01

Table 2. Results of similarity percentages analysis (SIMPER) of the differences in numerical fish composition in pellets of Great Cormorants at Lake Dümmer. Only seasonal comparisons that were significantly different in the ANOSIM are shown. Species with less than 5% contribution to the dissimilarity are not listed.

Season 1	Season 2	Average dissimilarity	Species	Contribution (%)	Mean relative abundance Season 1	Mean relative abundance Season 2
Autumn	Spring	36.32	Ruffe	38.79	0.673	0.395
			Roach	33.68	0.113	0.357
			Perch	7.85	0.117	0.104
			White Bream	7.25	0.016	0.067
Autumn	Summer	63.94	Pikeperch	46.95	0.034	0.634
			Ruffe	34.39	0.673	0.233
			Roach	8.29	0.113	0.007
			Perch	5.63	0.184	0.117
Winter	Summer	65.62	Pikeperch	48.03	0.008	0.634
			Ruffe	25.94	0.567	0.233
			Roach	10.56	0.143	0.007
			Perch	7.94	0.184	0.117
Spring	Summer	72.15	Pikeperch	43.82	0.002	0.634
			Roach	24.28	0.357	0.007
			Ruffe	17.02	0.395	0.233
			Perch	5.17	0.104	0.117

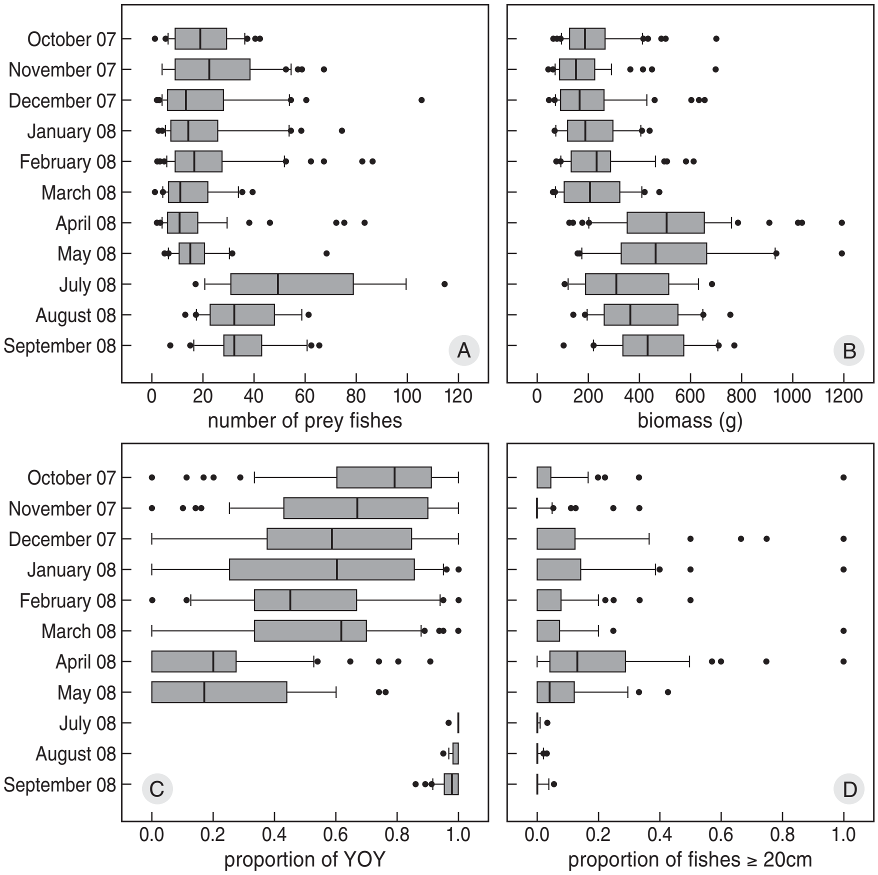


Figure 2. Box and whisker plots of monthly prey statistics per pellet of Great Cormorants at Lake Dümmer showing (A) number of prey fishes, (B) estimated biomass of prey fishes, (C) proportion of young-of-the-year fishes (YOY) and (D) proportion of large fishes ≥ 20 cm. Plots show medians (line), 25th and 75th percentiles (boxes), 10th and 90th percentiles (whiskers) and outliers (dots).

Biomass of prey fishes

The estimated ingested fish biomass from a single pellet averaged 320 ± 160 g (SD), with a maximum biomass of 1200 g per pellet. Biomass significantly differed between months, with the highest biomass found in April and May (Kruskal–Wallis $\chi^2 = 147.6$, $df = 10$, $P < 0.001$; Fig. 2B). Pairwise comparisons indicated significantly lower biomass in the pellets in the period of October–March compared to April–September (all P-values <0.01).

Proportions of YOY fishes and large fishes

The percentage of YOY fishes per pellet averaged 69.0 ± 24.9, but varied significantly in the course of the year (Kruskal–Wallis: $\chi^2 = 221.6$, $df = 10$, $P < 0.001$). More YOY fishes per pellet were found in July, August and September 2008 compared to the samples collected between October 2007 and May 2008 (post-hoc tests: all P's <0.001). The lowest proportions of YOY fishes were found in April and May 2008, while pellets collected during summer almost exclusively contained YOY-fishes (Fig. 2C). In April the proportion of fishes ≥20 cm in total length was significantly higher compared to all other months (Kruskal–Wallis: $\chi^2 = 92.1$, $df = 10$, $P < 0.001$, post-hoc tests: $P < 0.05$; Fig. 2D).

Prey species differences

The diet composition of Cormorants significantly differed between seasons (ANOSIM: global $R = 0.52$, $P < 0.001$). Differences were found between autumn and spring and between summer and all other seasons (ANOSIM: R-values >0.55, Bonferroni adjusted P's ≤ 0.002). Pikeperch, Ruffe, Roach, and Perch contributed most to the observed seasonal differences in diet (Table 2). Autumn and winter was dominated by Ruffe and unidentified Cyprinids, while in spring (particularly in April and May) Cormorants predominantly took Roach and White Bream. Pikeperch was the dominant

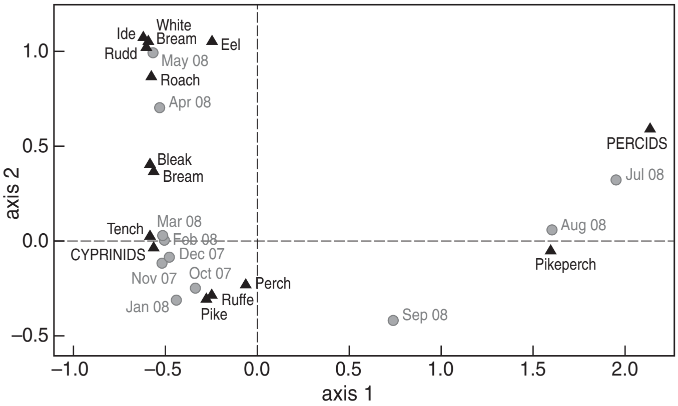


Figure 3. Biplot diagram of correspondence analysis showing the diet composition (relative numerical abundances of fish species) in the pellets of Great Cormorants at Lake Dümmer between October 2007 and September 2008. Prey species near certain months indicated characteristic prey at that time. Both axes combined explain 87.4 of the variability (axis 1: 74.4%; axis 2: 13.0%).

prey during summer with an average numerical abundance of 63.4% in the pellets (Table 2, Fig. 3).

Fish consumption

During the study period, total fish consumption of Great Cormorants at Lake Dümmer was calculated to be at least 32.6 tons, equivalent to 26.3 kg/ha. However, removal of fish biomass was not constant because of significant variation in the presence of birds and in DFI. The number of cormorant-days varied between 28,400 in October 2007 and 832 in May 2008 (Fig. 4A) and biomass removal varied between 0.35 and 9.5 kg/ha/month.

Four species accounted for 82% of the total biomass removal: Pikeperch (10.8 tons), Ruffe (6.5 tons), Perch (4.9 tons), and Roach (4.5 tons) (Fig. 4B), while 81% of Pikeperch biomass was taken in just two months (July, September 2008). Likewise, October 2007 and September 2008 accounted for approximately 70% of biomass removal of Ruffe and Perch. Although Roach was found to be the major prey at the time with the highest DFI (April, May 2008; Fig. 2B), both months had little impact on the total removal of Roach biomass (Fig. 4B) because of the low abundance of birds during these months (Fig. 4A).

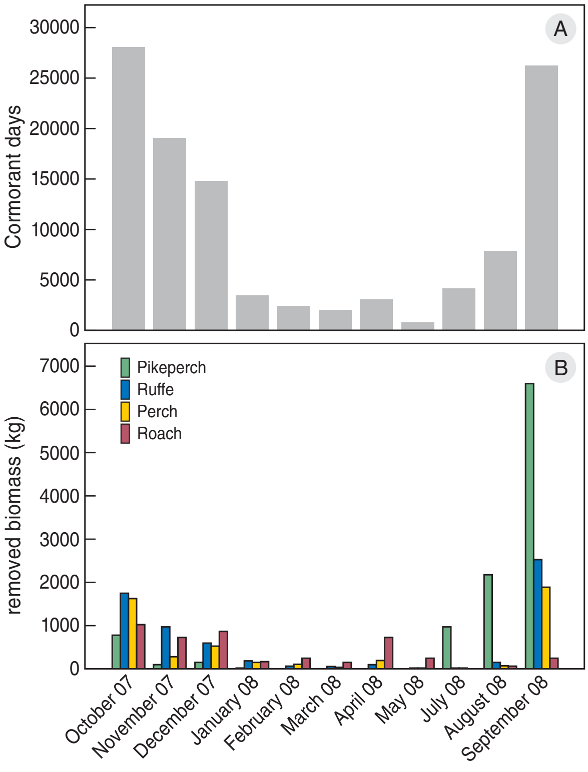


Figure 4. (A) Seasonal fluctuations of cormorant-days at Lake Dümmer from October 2007 to September 2008; (B) Estimated minima of monthly removal of the four dominating species Pikeperch, Ruffe, Perch and Roach. The four species accounted for 82% of the total biomass removal.

DISCUSSION

Seasonal changes in diet patterns

The diet of Great Cormorants at Lake Dümmer is in general consistent with that observed at other shallow, nutrient-rich lakes (de Nie 1995, Dirksen *et al.* 1995, Engström & Johnsson 2003). The relatively high numbers of small pelagic prey are known to be characteristic for social-hunting Cormorants as an adaptation to turbid environments (van Eerden & Voslamber 1995). Furthermore, the Cormorants' diet was dominated by all characteristic species generally dominating the fish communities of nutrient-rich lakes in the temperate zone of Europe, i.e. cyprinids: Roach, Bream, and percids: Ruffe and Pikeperch (Jeppesen *et al.* 2000, Mehner *et al.* 2007).

Many studies focusing on inland lakes found less clear patterns of prey fish selection by Cormorants (Suter 1997, Wziatek *et al.* 2003). In contrast, our statistical analyses indicated three distinct diet patterns of Cormorants at Lake Dümmer within a sampling period of eleven months:

Diet pattern in autumn and winter

The diet from October until March was dominated by unidentified small cyprinids and Ruffe, with no significant temporal changes in the frequency and biomass of prey items, and in the proportion of YOY and large fishes in the pellets. Ruffe, as a species with relatively large otoliths, is prone to be over-represented in pellet analysis, while small cyprinids are in general under-represented because of often complete dissolution of the small otoliths by gastric fluids (Zijlstra & van Eerden 1995, Martyniak *et al.* 2003). This makes interpretation of the results more difficult.

We think that the autumn–winter diet is an effect of limited availability of refuge structures, e.g. due to seasonal die-back of water-lilies, causing small cyprinids to aggregate and become more exposed, increasing availability to socially foraging Cormorants (van Eerden & Voslamber 1995). The occasional occurrence of large fishes in the Cormorants' diet at this time of the year might be caused by low water temperatures which reduce the swimming speeds of ectothermic fishes, enabling Cormorants to catch the larger fishes that are able to escape during summer (Čech *et al.* 2008).

Diet pattern in spring

In the breeding season (April, May) Cormorants predominantly foraged on cyprinids, in particular larger sized Roach and White Bream. Frequency of YOY fishes in the Cormorants' diet was lowest during these months. However, the number of prey items per pellet remained the same compared to autumn and winter, which resulted in a significant increase in the digested fish biomass. Several factors may explain the changes in prey fish patterns from autumn–winter to spring. Cormorant abundance can be an important factor affecting fishing behaviour and prey-fish selection with regard to composition and size. Low Cormorant abundance favours solitary-hunting, which, in general, results in larger fishes being caught (van Eerden & Voslamber 1995, Suter 1997, Santoul *et al.* 2004). Because in the present study we observed no significant changes in Cormorant abundance between January and May 2008, we have no evidence for an effect of differences in abundance on the changes in prey selection at this time of the year.

Energy requirements of Cormorants increase during incubation and parental care of nestlings (Grémillet *et al.* 1995). However, this cannot explain the higher food intake in spring, because many birds observed at Lake Dümmer in spring were non-breeding and immature individuals (M. Emmrich, unpubl. data).

Differences in prey availability as a consequence of changes in fish behaviour seem to be the likeliest explanation for the shift towards bigger cyprinids in spring. Aggregation and reduced escape distances during spawning facilitate Cormorants to depredate efficiently on larger fish that they could not catch outside the spawning periods, in particular at higher water temperatures (Magnhagen 1991, Čech *et al.* 2008). Diet studies on Cormorants in Bavaria and Switzerland showed that larger sized Whitefish *Coregonus* spp. and Grayling *Thymallus thymallus* were also predominantly caught during their spawning periods (Keller 1995, Suter 1997).

Diet pattern in summer

In summer (July–September) Cormorants fed almost entirely on YOY fishes which is not surprising in view of the abundance of small-sized fishes at this time of the year (Wolter & Pawlizki 2003). The increase in digested fish biomass within this period can be explained by the growth of juvenile fish during summer. In contrast to our results, Dirksen *et al.* (1995) found the lowest DFI of Great Cormorants at shallow eutrophic lakes within the summer period, which was interpreted as poor foraging success of young, inexperienced birds. However, Lake Dümmer is largely frequented by immature and a few adult birds at this time of the year. It is most likely that the high foraging success of young Cormorants is caused by easily accessible prey, specifically YOY fishes lacking experience of predators. Indeed, during summer the Cormorants almost exclusively fed on juvenile Pikeperch at Lake Dümmer. Dominance of a single prey species is typically observed at fish ponds (Lekuona 2002, Farago *et al.* 2006) or sometimes recorded for Ruffe in natural waters (Engström 2001, Martyniak *et al.* 2003), but rather exceptional for top-predatory fishes such as Pikeperch. We assume that the strong occurrence of Pikeperch in the Cormorants' diet during summer did not result from methodical inadequacies (i.e. overrepresentation), as the delicate otoliths are in general more vulnerable to wear (Marteijn & Dirksen 1991, Zijlstra & van Eerden 1995). We suppose that the strong occurrence of YOY Pikeperch reflects both high abundances and high predation sensitivity of juvenile Pikeperch in summer because, like other percids, small Pikeperch aggregate in shoals (de Nie 1995).

Cannibalism in Pikeperch is a frequently observed phenomenon, which sometimes is the primary force for recruitment success. Frankiewicz *et al.* (1999) showed that cannibalism lead to a strong decline of YOY Pikeperch in late summer and Smith *et al.* (1996) found only strong YOY cohorts in the presence of low abundances of adult conspecifics (>37.5 cm fork length). This could explain why catches at Lake Dümmer revealed high abundances of small Pikeperch ≤ 20 cm (9.9% of the total gillnet catch in 2007) but just a few individuals exceeding the size threshold reported by Smith *et al.* (1996; M. Kämmereit, unpubl. data). Likewise, only 0.6% of all Pikeperch (n = 1692) found in the Cormorant pellets exceeded lengths of 20 cm. Both results support the assumption of extremely low abundances of larger Pikeperch in Lake Dümmer, which in turn leads to apparently high survival rates of conspecifics early in ontogeny. In September, Ruffe and Perch became more dominant in the Cormorants' diet, probably as a consequence of a reduction in the continuously exploited juvenile Pikeperch stock.

Biomass removal

Using data from pellet analyses to determine DFI of Cormorants has been criticized because of incomplete recovery rates of diagnostic prey structures from pellets causing underestimates of DFI (Mc Kay *et al.* 2003). However, it is not possible to quantify this error for free-living Cormorants, and studies on birds kept in captivity show contrasting results (Zijlstra & van Eerden 1995). Nevertheless, we do not expect that this bias will seriously affect the seasonal patterns in DFI that we describe.

We estimated DFI in the period April–September 2008 to average 442 g, which is close to the per-capita consumption of 436 g/day estimated in a meta-analysis by Ridgeway (2010). Therefore, estimates of fish removal during this period do not seem to be strongly biased. In contrast, the low estimates of biomass from pellets collected between October 2007 and March 2008 is not easily explained. Biomass estimates from pellets from October 2007 and September 2008 differed substantially. It is likely that this was caused by year-to-year differences in the abundance of YOY fishes. The recruitment success, in particular of Pikeperch, was probably lower in 2007 compared to 2008 and resulted in a lower food intake until spring when Cormorants shifted to larger fish that aggregate during spawning.

Conclusion

Our study indicates that the diet of Cormorants foraging at an inland lake can substantially vary with season in species composition, number and size range of fish taken. In winter the diet was dominated by small-sized cyprinids and Ruffe. During spring, larger fishes were taken, possibly due to their increased vulnerability to predation during the spawning period. In contrast, during late summer, young-of-the-year percids dominated, with Pikeperch as the most abundant species. Our findings emphasize the need for extensive diet analyses considering all seasons to obtain a comprehensive picture of predation by Cormorants and its impact on fish stocks. Snapshots of diet taken over short-time periods may be misleading and inadequate for local management decisions.

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SAMENVATTING

De auteurs onderzochten de voedselsamenstelling van Aalscholvers *Phalacrocorax carbo sinensis* die foerageerden op het Dümmermeer, een ondiep, voedselrijk meer van 1.240 ha in Neder-Saksen, Duitsland. Zij verzamelden verspreid over een heel jaar in totaal 562 braakballen, die daarna nader werden onderzocht. De braakballen bevatten skeletdelen van 10.645 vissen behorende tot 15 soorten. Er werden in de loop van het jaar substantiële verschuivingen in de frequentie, samenstelling en grootte van de gegeten vissoorten gevonden. Snoekbaars *Sander lucioperca*, Pos *Gymnocephalus cernuus*, Blankvoorn *Rutilus rutilus* en Baars *Perca fluviatilis* veroorzaakten de grootste seizoensverschillen in het voedsel. In de late herfst en winter werd het voedsel gedomineerd door kleine karperachtigen en Pos. In het voorjaar foerageerden de Aalscholvers voornamelijk op grotere karperachtigen. In de zomer vormden jonge baarsachtigen (voornamelijk Snoekbaars) de voornaamste prooi. De auteurs schatten dat ten minste 32,6 ton (26,3 kg/ha) vis door Aalscholvers werd geconsumeerd, waarvan een derde (10,8 ton) bestond uit Snoekbaars. In augustus–september werd 81% van de in dat jaar geconsumeerde hoeveelheid Snoekbaars aan het meer onttrokken. Dit geeft aan dat de Aalscholvers in het Dümmermeer een belangrijke predator van jonge Snoekbaars is. Deze bevindingen laten zien dat het noodzakelijk is om in alle seizoenen een uitgebreide voedselanalyse uit te voeren. Anders wordt geen goed beeld verkregen van de invloed die predatie door Aalscholvers heeft op de visstand. Kortstondige metingen aan de voedselsamenstelling kunnen misleidend zijn en leiden tot inadequate beheersmaatregelen. (PW)

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Appendix 1. Linear regressions (Y = a x + b) and coefficient of determination (R^2) of fish total length (TL; cm) and relevant key-structures (mm) for the prey-fish identification from Lake Dümmer fishes. Furthermore, regressions of the length–weight relationship W = aTL^b for the back calculation of prey-fish weight (W; g) from total length (TL; cm) are given.

Species	*n*	Size range (cm)	Regression[a]	R^2	Length–weight	R^2
Pikeperch *Sander lucioperca*	59	10.4–38.3	TL = 4.6879 S – 4.6704	0.93	$W = 0.004011\ TL^{3.1758}$	0.98
			TL = 0.8732 PO + 0.6564	0.96		
			TL = 0.6407 O – 0.0677	0.94		
			TL = 1.1481 D – 1.7277	0.96		
Ruffe *Gymnocephalus cernuus*	64	5.4–18.5	TL = 2.2696 S – 0.0459	0.97	$W = 0.005866\ TL^{3.2087}$	0.99
			TL = 0.9482 PO – 0.2658	0.98		
			TL = 1.1833 O + 1.0345	0.97		
Perch *Perca fluviatilis*	47	5.7–27.1	TL = 3.8436 S – 3.7800	0.94	$W = 0.005889\ TL^{3.2294}$	0.99
			TL = 0.8824 PO + 0.5559	0.98		
			TL = 1.1002 O + 1.3692	0.98		
Roach *Rutilus rutilus*	46	8.1–28.8	TL = 9.2646 S – 4.8826	0.98	$W = 0.002879\ TL^{3.4324}$	0.99
			TL = 1.6603 P_s + 0.3244	0.99		
			TL = 1.5352 P_g + 2.2416	0.99		
White Bream *Blicca bjoerkna*	45	7.5–27.7	TL = 10.0890 S – 6.3752	0.96	$W = 0.007432\ TL^{3.1204}$	0.99
			TL = 1.7802 P_s + 0.3591	0.98		
			TL = 2.1475 P_g + 0.2174	0.95		
Bream *Abramis brama*	27	6.8–30.1	TL = 9.9592 S – 5.1670	0.99	$W = 0.003901\ TL^{3.2480}$	0.99
			TL = 1.6951 P_s + 0.1201	0.99		
			TL = 2.5785 P_g + 0.1550	0.94		
Ide *Leuciscus idus*	6	10.5–32.6	TL = 10.6163 S – 7.5733	0.98	$W = 0.003102\ TL^{3.3335}$	0.98
			TL = 1.6152 P_s – 0.7387	0.99		
			TL = 1.9512 P_g – 0.8425	0.99		
Rudd *Scardinius erythrophthalmus*	11	14.6–28.7	TL = 9.9624 S – 6.3802	0.95	$W = 0.003633\ TL^{3.4106}$	0.99
			TL = 1.5386 P_s + 0.5171	0.99		
			TL = 1.6041 P_g + 2.1556	0.99		
Tench *Tinca tinca*	18	10.2–25.3	TL = 13.8407 S – 8.9970	0.94	$W = 0.01425\ TL^{2.9877}$	0.99
			TL = 1.3323 P_s – 0.2690	0.99		
			TL = 1.6626 P_g + 0.2818	0.98		
Bleak *Alburnus alburnus*	12	9.8–17.5	TL = 6.4071 S + 2.5328	0.88	$W = 0.002524\ TL^{3.3554}$	0.95
			TL = 2.1435 P_s – 0.14168	0.84		
			TL = 1.7755 P_g + 5.3007	0.88		

[a] Measured structures: S = otolith (*saggitus*); PO = preopercular (*praeoperculare*); O = opercular (*operculare*); D = lower jaw (*dentale*); P_s = pharyngeal bone (*os pharyngeum*), shank measured; P_g = pharyngeal bone (*os pharyngeum*), gape measured.

For illustrations of pharyngeal-bone measures see Prenda *et al.* (2002).