

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

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ABSTRACT During the period October 1989 - April 1992 a study on Cormorant feeding ecology was carried out in two shallow lakes in The Netherlands: lake Veluwemeer and lake Wolderwijd (3240 and 2600 ha respectively). Increasing numbers of Cormorants use these lakes for feeding in the non-breeding season; the maximum number, usually reached in October or November, amounted to 1314 in 1991. The effect of Cormorant predation on fish stock was studied for two reasons: assessing possible damage to commercial fishery and assessing the role of the birds in a large-scale biological management programme that has been carried out in lake Wolderwijd during the period of study. As part of this programme, fish stock in this lake was reduced from 203 to 46 kg/ha. Most important prey species was Ruffe (60% of fish-mass in 1991/92), which has no value to either commercial fishermen or anglers. Perch, Pikeperch, Roach and Smelt were found in most samples as well, while Eel, the only species commercially caught in the lakes, was hardly found at all. Mean daily intakes ranged from 146 to 699 g with highest values in October and March. In 1989/90 total consumption in the two lakes was estimated at 3.7 kg/ha. In September 1991 - March 1992 however, after fish removal, 80% went to lake Wolderwijd, where smaller fish were taken. Nevertheless, total consumption amounted to 12.5 kg/ha, against 2.1 kg/ha in lake Veluwemeer. As most of the fish consumed belongs to species potentially hazardous to water quality (transparency) the Cormorants seem to support biological management. It is discussed whether the larger proportion of small, shoaling fish after removal of large fish could have enhanced possibilities for mass flock fishing, attracting the birds to lake Wolderwijd. On the other hand, achieving the long-term goals of biological management is likely to reduce the fishing possibilities for Cormorants.

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INTRODUCTION

In northwest Europe, numbers of Cormorants *Phalacrocorax carbo sinensis* have increased sharply over the last decades (Van Eerden & Gregersen 1995). Simultaneously, an increasing number of Cormorants has been spending the winter in The Netherlands. Until recently, studies on the feeding ecology and food choice of

Cormorants in NW Europe have been focussed on the breeding season. In The Netherlands for example, studies of the food choice of this piscivorous bird species have been published by Van Dobben (1952), De Boer (1972), Voslamber (1988), Platteeuw (1988), Dirksen *et al.* (1989) and Veldkamp (1991, 1995a). Data from the non-breeding period have been published for the Camargue, France (Im & Hafner 1984), water bodies in

Switzerland and Bavaria, southern Germany (Suter 1991, Keller 1995) and lake Ketelmeer in The Netherlands (Platteeuw *et al.* 1992).

There is a common interest of Cormorants, anglers and commercial fishermen in the fish stock of Dutch water bodies. Therefore, a study of food and factors influencing prey choice and biomass taken during the non-breeding period provides a baseline for future decisions on nature and fisheries management. Such a study, concerning both lakes and rivers, has been started in 1989. This paper presents the results obtained from two shallow lakes: lake Wolderwijd and lake Veluwemeer.

Results of studies on feeding ecology of Cormorants can also be used in biological water management in relation to eutrophication. During the research period a large scale biological water management plan has been carried out in lake Wolderwijd (Hosper & Jagtman 1990, Meijer *et al.* 1990). Until 1990 this lake contained a large amount of Bream *Abramis brama* and other benthivorous fish that stirred up bottom material in search of food. Together with blooms of blue-green algae, and heavy predation on zooplankton, this habit drastically reduced transparency. As part of a plan to reduce eutrophication and to enhance transparency, fish biomass was artificially reduced by more than 75% during the period November 1990 - July 1991 and additional fisheries have been carried out since then (Van Nes *et al.* 1992). These measures are likely to have had an effect on Cormorant food availability and composition. On the other hand, consumption by the birds may influence the outcome of this experiment. The second aim of the project therefore was to study the Cormorant's response, and to gather information to enable a discussion on their relationship to water quality management.

STUDY AREA

As a result of large-scale embankments of lake IJsselmeer in the period 1957-68 a series of shallow (1-2 m) freshwater lakes was created

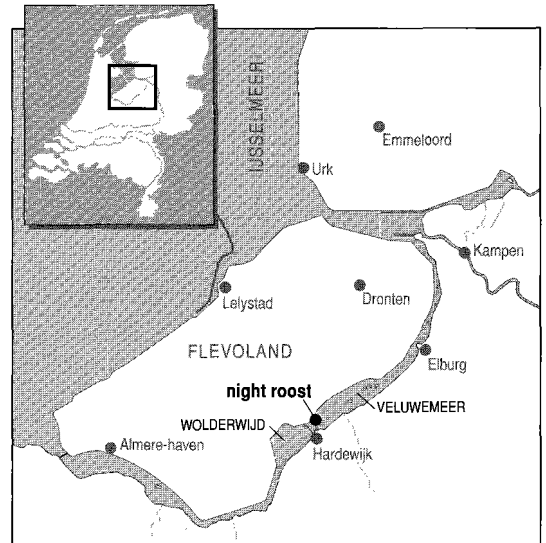


Fig. 1. The study area (Lake Wolderwijd and Lake Veluwemeer) with the location of the night roost used by Cormorants.

(Fig. 1). Two of these lakes are lake Wolderwijd (2600 ha) and lake Veluwemeer (3240 ha), which play an essential role in water management of the Flevopolders. They are important to agriculture and indirectly they supply a source for drinking water production. The lakes are used for recreation and for fishery, both commercial fishery for Eel and recreational angling for other species. They also have a pronounced ecological function, as a habitat for submerged macrophytes which attract both fish (spawning, cover) and herbivorous waterbirds like Bewick's Swans *Cygnus columbianus bewickii*.

These lakes can be characterised as eutrophic and since 1970, as a result of high nutrient levels, blooms of blue-green algae regularly occur. Mean water transparency rarely exceeded 50 cm Secchi disc in winter until 1991. In summer transparency was often 30 cm or less.

Despite the relatively bad light conditions, nowadays submerged macrophytes occur in 35-40% of the total area of both lakes from May to September (though only 10-15% with more than 15% coverage). The waterplant community is

dominated by pondweeds *Potamogeton pectinatus* and *P. perfoliatus* (De Redelijkheid & Scheffer 1990, Doef *et al.* 1991), in 1992 partly replaced by *Chara* spp.

Several measures have been taken to improve water quality, including flushing with water from the adjacent Flevopolders, which has lower nutrient contents, and large-scale fish removal in lake Wolderwijd. In both lakes nutrient levels have dropped, but in lake Veluwemeer this has not yet led to an increase in transparency. In lake Wolderwijd transparency improved to a maximum of 180 cm after the fish removal in spring 1991, but this situation lasted only for about two months (Van Nes *et al.* 1992).

FISH STOCK

Backx (1989a, b) described the development of fish stocks in both lake Wolderwijd and lake Veluwemeer during 1966-1987. In both lakes fish stock became dominated by Bream (more than 80% of total fish biomass), associated with an almost continuous dominance of bluegreen algae (mainly *Oscillatoria agardhii*) from *c.* 1970 onwards (Berger 1987). Pikeperch *Stizostedion lucioperca* was the second most important species (*c.* 10 %). Roach *Rutilus rutilus*, Ruffe *Gymnocephalus cernuus*, Perch *Perca fluviatilis*, Eel *Anguilla anguilla* and Smelt *Osmerus eperlanus* were less numerous. From 1983 onwards, after some improvement in water quality, strong year-classes of Roach and Perch were found, although Bream still remained by far the most abundant species (70-85% of biomass). Pikeperch decreased to about 3% of the biomass.

For lake Wolderwijd, all available data on fish biomass from 1989-1992 have been summarised in Table 1. Based on the series of data used by Backx (1989a,b), in combination with sampling by Witteveen+Bos (1989, 1990) and Lammens & Vlink (1990), a total of *c.* 210 kg fish/ha was estimated for lake Wolderwijd in February-May 1989 (Meijer 1989, pers. comm.). Roach was probably much more important than estimated before,

although Bream still took the largest share of biomass.

Sampling in 1990 showed a large amount of cyprinid fry, and less large Roach and more large Bream than the previous year. Between November 1990 and July 1991, 425 tons of fish (*c.* 157 kg/ha) were removed from lake Wolderwijd. The original stock in November 1990 was estimated at 203 kg/ha (Eel excluded), which was reduced to 46 kg/ha in June 1991. More than half of the fish removed was Bream (97 kg/ha), especially large ones (> 25 cm; 74 kg/ha). Ruffe turned out to be much more abundant than estimated before; about 25 kg/ha was removed. By July the total amount of fish had increased again to 92 kg/ha, largely caused by an estimated 29.5 kg/ha of 0+ Ruffe. In September 1991 10.1 kg/ha of cyprinid fry was found and total fish biomass amounted to 125 kg/ha. In April 1992, after additional fisheries during winter, 74 kg/ha remained. In May 1991 small Pike *Esox lucius* were released to suppress recruitment of benthivorous species.

In lake Veluwemeer no large-scale fish removal was carried out, and probably no major changes occurred in the fish stock during the study period.

METHODS

Counts of waterbirds have been carried out at least monthly by the Ministry of Agriculture, Nature Management and Fisheries since the construction of the lakes. From October 1989 onwards we organised bi-weekly counts at the roost in the southwestern part of lake Veluwemeer. In 1991/92 observations of number and direction of foraging flights from the roost were carried out in order to determine the proportion of Cormorants foraging in both lakes (2-4 days every month), since the fish stocks in the lakes were no longer comparable. Furthermore, additional observations of foraging groups were obtained from several observers.

Almost every month from October to March 1989-1992, and in August and September 1992,

Table 1. Estimates of fish biomass (kg/ha) in lake Wolderwijd, 1989-92. Data from Witteveen+Bos (1989, 1990), Backx *et al.* (1992), Grimm *et al.* (1992), Backx (1992). Estimates were made using different types of fishing gear and are corrected for their efficiency. Also species-specific distribution patterns within the lake were taken into account. If ranges were given, the median is put in the table. From November 1990 onwards the catch during fish removal could be used for estimations; the first two estimates are less accurate. For Roach and Bream size class is given in cm.

year month/period	1989 Feb/ May	1990 Mar/ Jul	1990 Nov	1991 Jun ¹	1991 Jul	1991 Sep	1992 Apr ²
Roach/Bream 0-14		77			3.5	10.1	
Roach 0-14			23.5	5.3	6.7	4.9	7.1
Roach >14	80	5	15.6	3.5	6.4	4.5	1.5
Bream 0-14			21.2	4.8	1.5	0.9	4.6
Bream 15-24	40	8.5	8.6	1.9	2.0	20.0	15.0
Bream >24	60	89.5	95.6	21.5	23.4	25.6	23.4
fry, all species		10					
Perch/Pikeperch	7.5	2.5					
Perch			3.2	0.8	5.0	3.9	3.7
Pikeperch			1.0	0.1	3.2	2.7	1.9
Ruffe			32.8	7.4	38.5	40.5	15.0
Smelt			1.5	0.3	0.5	2.1	1.3
Total	210.0 ³	205.0 ⁴	203.0	45.6	91.9 ⁵	115.8 ⁵	73.9 ⁵

¹Figures for June 1991 are obtained by subtracting the amount of removed fish for each category from the estimates of November 1990.

²Figures for April 1992 are obtained by subtracting the amount of removed fish for each category from the estimates of September 1991. Losses by Cormorant predation are not accounted for.

³Including 10 kg of Ruffe and Smelt and 12.5 kg of Eel.

⁴Including 12.5 kg of Ruffe, Smelt and Eel. Eel is not included in totals from 1990 onwards.

⁵Including Three-spined Stickleback (1.2, 0.6 and 0.5 kg respectively).

20-30 complete and fresh pellets were collected at the roost (Appendix 2). All pellets from one date will be referred to as one sample. A detailed description of the analysis of pellets has been given by Marteijs & Dirksen (1991). Therefore, only a short outline will be given here.

Fish remains (otoliths, jaws, pharyngeal bones, operculae, cleithra) were identified using reference collections. The number of individuals of a species represented in a pellet was defined as the highest total of any of the identifiable parts present, taking right and left parts separately. A

correction was made when the sizes of otoliths or the presence of other remains indicated that (an) individual(s) was (were) not included this way. The length of otoliths and pharyngeal bones was measured, and from these the total length and mass of each fish were calculated using regression formulae (Appendix 1). Since the regression between otolith/pharyngeal bone length and fish length concerns two measurements of structural size, no special attention was paid to the site and time these fish were caught. This is different for the regressions involving body mass, as the ratio

length/body mass changes throughout the year. Length-mass regressions were obtained from fish caught in lake Wolderwijd throughout the winter season (Appendix 1). The data on fish-mass for 1989-90, which were presented by Marteijn & Dirksen (1991), have been recalculated using these more accurate regressions.

Otoliths of cyprinids could not be identified to the species-level. Individuals of this family were either identified by pharyngeal bones (whenever present), or entered as unidentified cyprinid. Most of these unidentified cyprinids belonged to the 0+ year class. At the end of the summer of 1989 75% of all young fish in the Wolderwijd consisted of Bream and Roach, of which 25% was Roach (Lammens & Vlink 1990). Therefore, it is likely that nearly all small cyprinids in the pellets belonged to these two species, probably with Bream dominating. For both species the regression between otolith length and fish length was inaccurate in small individuals. Because of this, these first year Roach/Bream were assumed to weigh 1.3 g (otoliths < 1.5 mm). For somewhat larger individuals (otoliths 1.5-2 mm, e.g Roaches < 11 cm) a standard mass of 12 g was used. For unidentified cyprinids with otoliths > 2 mm, regressions for Roach were used in body mass calculations, because 92% of individuals of which pharyngeal bones were present belonged to this species. Only when pharyngeal bones of the other species have a higher chance of being dige-

sted in the Cormorant's stomach this may cause inaccuracies, which will be discussed later.

RESULTS

Cormorant numbers

In recent years numbers of Cormorants wintering in The Netherlands have increased sharply. Total numbers in mid-winter increased from below 1000 in 1980 to over 7000 in 1989 (Buesink *et al.* 1992). Unfortunately the Cormorant was not included in these mid-winter censuses before 1980, but wintering numbers in the seventies must have been restricted to a few hundred. During the 1970s numbers in lake Wolderwijd and lake Veluwemeer were highest in August and September and amounted to around 250 at the most (Table 2). When in the mid-80s fish biomass in the lakes strongly increased, Cormorant numbers showed an increase beyond the national trend. Since then counts of around 1000 individuals are no exception. Highest numbers occur in October and November. The increase in fish biomass was stronger in lake Wolderwijd, and the proportion of the birds foraging in this lake increased as well (Table 2).

Throughout the study period one single roost was used, situated in lake Veluwemeer. The birds were either sleeping in pylons or in trees on the small island 'Krooneend' nearby (Fig. 1). From

Table 2. Maximum numbers of Cormorants in lake Veluwemeer and lake Wolderwijd (during daytime, including roost) and proportion seen foraging in lake Wolderwijd (%WW) in autumn, winter and spring. Counts of less than 100 individuals are shown in parentheses (data from: Ministry of Agriculture, Nature Management and Fisheries, Directorate NBLF).

period	autumn		winter		spring	
	tot.	%WW	tot.	%WW	tot.	%WW
1970 - 1974	198	8.2	16	(47.7)	80	(48.8)
1975 - 1979	225	13.2	75	(13.4)	111	21.2
1980 - 1984	150	15.8	206	7.3	258	19.5
1985 - 1989	872	15.0	965	20.4	654	40.4
1990 - 1992	735	28.6	427	36.0	1012	52.6

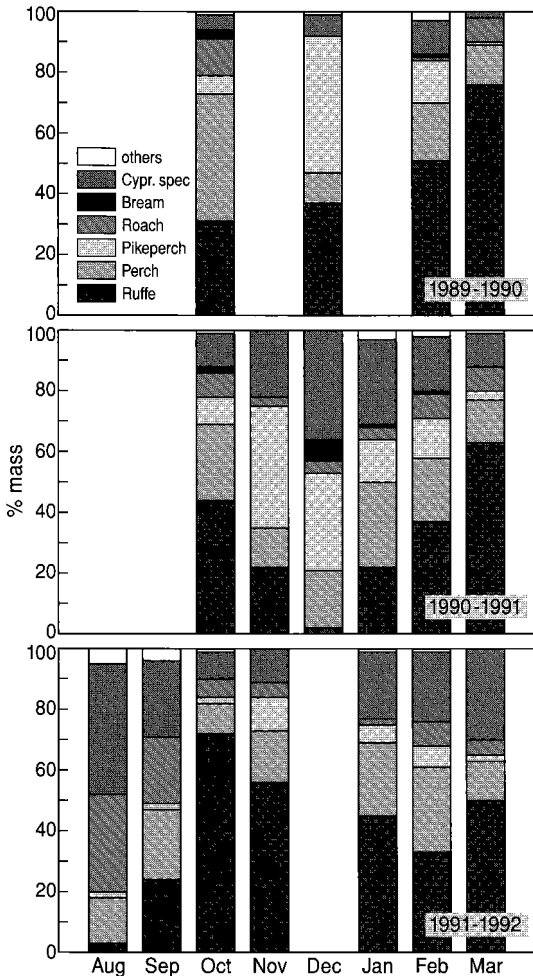


Fig. 3. Mass (%) according to fish species in pellets of Cormorants, Lake Wolderwijd / Lake Veluwemeer 1989-1992 (for sample size see appendix 2).

consisted of percids (Fig. 3). Cyprinids accounted for 10-40% and Eel, Pike and Smelt together were always below 3%. Some seasonal patterns can be distinguished in the mass composition of the pellet samples. In 1991/92, the proportion of Ruffe increased from a few percent in August to 73% in October, then decreased slowly throughout the winter to 33% in February and increased again in March. The pattern between October 1990 and March 1991 was comparable, but the minimum was earlier and lower (2% in December). In

1989/90 the proportion of Ruffe in October was relatively low (30%) and only increased from that time on. The relative pattern of Pikeperch was comparable in all three winters: in November and December a high proportion of the total fish-mass consisted of Pikeperch, with lower proportions before and afterwards.

In 1989/90 and 1991/92, almost all Ruffe and Perch eaten was of age 0+ (4-9 and 4-10 cm resp.). In 1990/91 however, quite a lot of 1+ individuals were taken as well (Fig. 4). The maximum length of Perch caught was 29 cm. The data on Pikeperch (Fig. 4) show a gradual shift over the year classes 0+, 1+ and 2+ in 1989/90 to a clear dominance of 0+ (4-14 cm) in the pellets in 1991/92. The maximum size was 38 cm. Roach also shows a shift towards smaller individuals in the third winter (Fig. 4). This effect is even stronger than shown in the figure, as small individuals are underestimated here (see below, Table 3). The largest Roach taken was 31 cm. Nearly all Smelt in the pellets were 0+ (4-8 cm), but some 1+ individuals were present as well. Of the species less frequently caught, Bream were taken up to a length of 27 cm, but most individuals were 1+ (10-13 cm). All Ides in the pellets were relatively large: 19-26 cm ($n = 7$). Both small and

Table 3. Number of cyprinids in the pellet samples according to age/species identification-level maximally achievable.

	1989- 1990	1990- 1991	1991- 1992
not identified to species			
cyprinid species, 0+	123	1015	1705
cyprinid species $\geq 1+$	57	190	321
species identification possible (mainly $\geq 1+$)			
Bream	3	21	4
Roach	44	158	302
Carp, Ide, Rudd	1	4	10
total	228	1388	2342

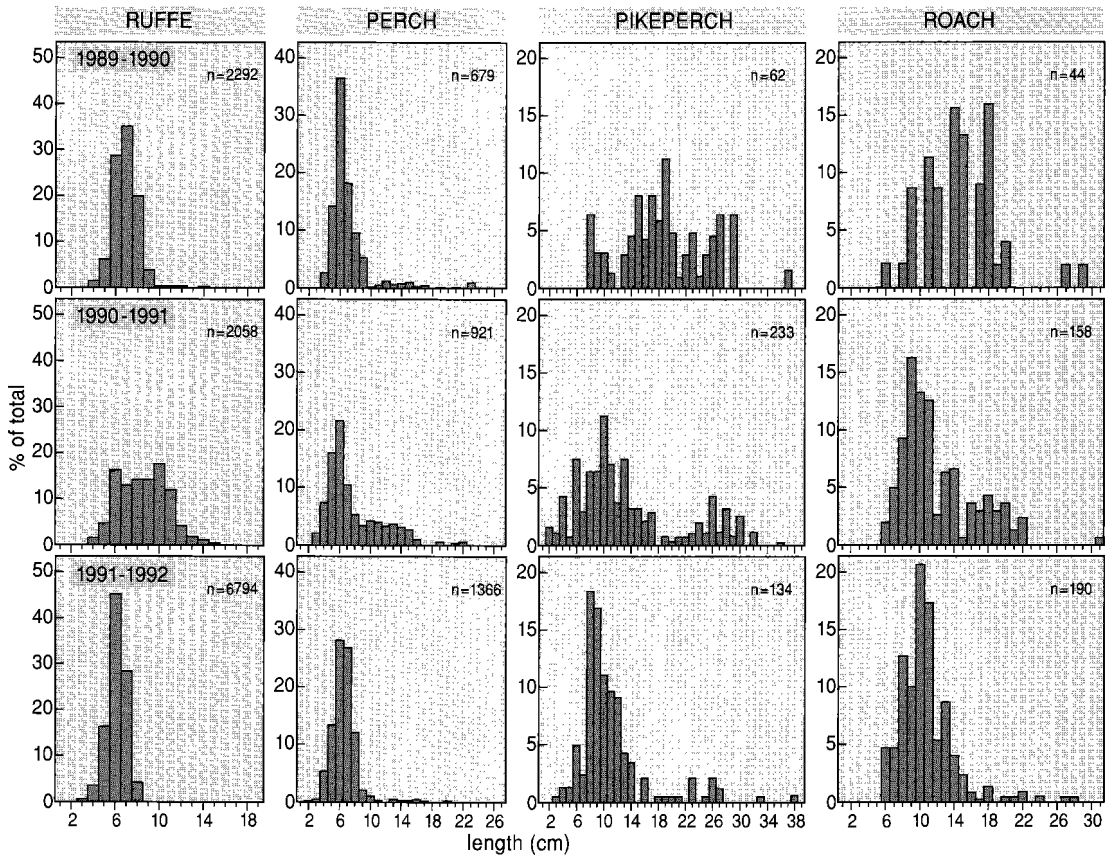


Fig. 4. Length-frequency distribution of (a) Ruffe, (b) Perch, (c) Pikeperch and (d) Roach caught by Cormorants in Lake Wolderwijd / Lake Veluwemeer in October - March 1989-1990, 1990-1991 and 1991-1992.

larger Rudd were caught (8-24 cm, $n = 3$), and only small Carps (4-9 cm, $n = 5$). The Pike found in the pellets were between 3 and 20 cm ($n = 6$). Finally, Eel ranging from 24 to 44 cm ($n = 5$) were caught.

Unidentified cyprinids were quite numerous sometimes (up to 50%) but in most samples they accounted for 10-30% of all fish. On a mass basis, 10-35% was found in most samples. The majority of unidentified cyprinids consisted of 0+ fish. Nevertheless 50-55% of $\geq 1+$ cyprinids could not be identified either (Table 3). Probably most of these were Roach, as were most of the individuals of which pharyngeal bones were found. However, Veldkamp (1995a & b) suggests that pharyngeal bones of Bream have a higher chance to disappear

than those of Roach, and the group of unidentified $\geq 1+$ cyprinids may therefore contain a relatively high number of Bream.

Daily intake As a consequence of the small size of the fish taken, the mean number of fish per pellet is relatively high in most samples: means of 40-60 fish/pellet are quite common (Appendix 2). The highest mean is 171 fish/pellet in October 1991, with many pellets containing as many as 200 to a maximum of 313 fish.

The mean estimated total fish-mass per pellet (assumed to equal mean daily intake per bird) in the samples varied between 146 and 699 g (Appendix 2). The variance within samples was substantial, but the frequency distributions

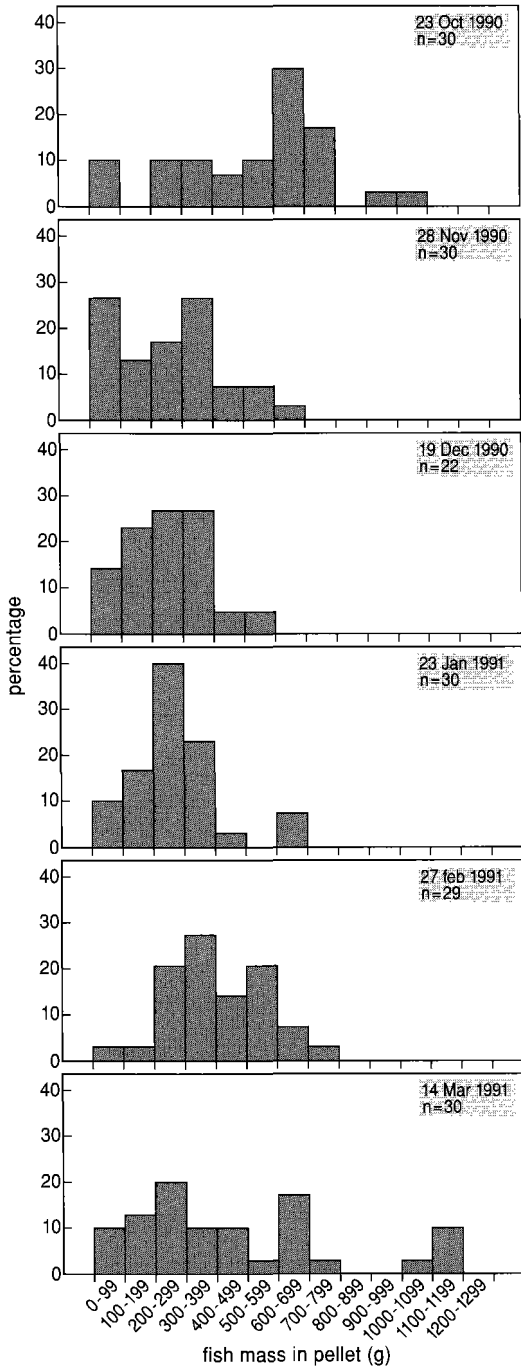


Fig. 5. Frequency-distributions of total fish mass (g) in monthly samples of pellets, Lake Wolderwijd / Lake Veluwemeer 1990-1991.

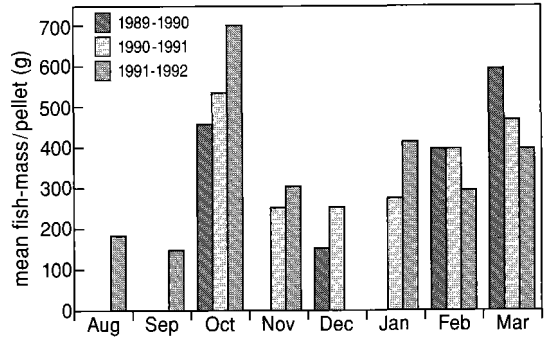


Fig. 6. Mean fish mass in pellets of Cormorants, Lake Wolderwijd / Lake Veluwemeer 1989-1992 (see also Table 4).

normally were unimodal and rather smoothly shaped (data from 1990/91 as example in Fig. 5). Fish-mass over 1 kg/pellet typically occurred in the three March-samples (respectively 13, 13 and 16% of the samples) and in October 1991 (15%). There seemed to be a comparable pattern in all three seasons: high daily intakes in October, lower values in November and December, followed by an increase from January to March (Fig. 6). Intake in October increased from 1989/90 to 1991/92 ($p = 0.0012$, Mann-Whitney U-test), while the February and March means showed a reverse trend (though not statistically significant: $p = 0.11$ for February and $p = 0.12$ for March).

Total fish consumption in relation to fish stock
 Using the data on Cormorant numbers and food composition presented above, total fish consumption in the non-breeding period can be estimated (Table 4). In 1989/90 fish stocks in both lakes were comparable (Backx 1989a, b). Moreover, observations on the choice of feeding areas of the roosting Cormorants are not available. The consumption therefore has been estimated for the two lakes together. For 1991/92 the proportion of Cormorants choosing each lake was known from observations, and fish consumption could be estimated for the two lakes separately. As the majority foraged on lake Wolderwijd, the data from the pellets have been taken as representative for the diet taken from this lake. For lake Veluwemeer

Table 4. Estimated total fish consumption (kg) and predation pressure (kg/ha) by Cormorants, lake Wolderwijd (WW) and/or lake Veluwemeer (VM). nc: not calculated, see text.

period	Oct 1989/ Mar 1990		Sep 1991/ Mar 1992		Sep 1991/ Mar 1992	
	kg	kg/ha	kg	kg/ha	kg	kg/ha
area	WW + VM		WW		VM	
surface (ha)	5840		2600		3240	
bird-days	62373		74881		20977	
Eel	70	0.0	-	-	-	-
cyprinids	3574	0.6	6791	2.6	nc	nc
Pike	32	0.0	10	0.0	nc	nc
Smelt	83	0.0	383	0.1	nc	nc
Ruffe	8632	1.5	19237	7.4	nc	nc
Perch	6621	1.1	4783	1.8	nc	nc
Pikeperch	2786	0.5	1378	0.5	nc	nc
total	21797	3.7	32482	12.5	6826	2.1

Consumption estimated as sum of estimates for two-week-periods:

$\Sigma N_d \cdot N_c \cdot P_a \cdot W \cdot P_x$, where:

N_d = number days in period

N_c = number Cormorants on roost

P_a = proportion of roosting Cormorants feeding in area concerned

W = mean fish-mass in pellet (kg)

P_x = proportion of fish-mass of species x in sample

only an estimate for total consumption has been calculated.

In 1989/90 the Cormorants took an estimated 3.7 kg fish/ha from lake Wolderwijd and lake Veluwemeer, of which 40% was Ruffe. For lake Wolderwijd in 1991/92 the estimated consumption was 12.5 kg/ha, of which 60% was Ruffe. The difference with 1989/90 is caused by higher numbers of Cormorants as well as a higher daily intake per bird. For lake Veluwemeer an estimate of 2.1 kg/ha was calculated for 1991/92.

Neither in 1989/90 nor in 1991/92 did the diet composition of the Cormorants reflect the relative densities of the fish species present. In 1989/90 especially the large amounts of $\geq 1+$ Bream and Roach present in the lakes were almost completely absent from the diet (Table 1, Fig.3),

although in this season a relatively large part of the Roach consumed was 1+ (Fig. 4). In 1991/92 the large fish had been strongly reduced (Table 1), and large Bream (≥ 24 cm), even though still c. 25 kg/ha was present, was not found at all in the pellets. In both seasons Ruffe and Perch on the other hand were caught in much higher proportions than their relative abundance among the stock would indicate (Fig. 7).

DISCUSSION

The method of pellet-analysis

Authors stating one pellet is produced each day (Van Dobben 1952, Miller 1979) are supported by trials with captive Cormorants by Zijlstra &

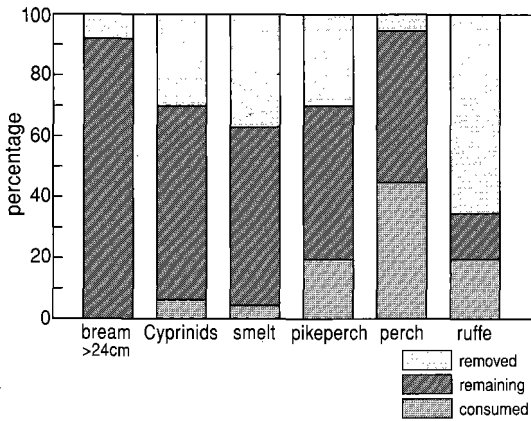


Fig. 7. Consumption of several fish species by Cormorants and the amount of fish removed by fishermen during the period September 1991 - March 1992, as percentages of estimated stock in September 1991 (Backx *et al.* 1992, Grimm *et al.* 1992; see Tables 1 and 4). Most large Bream had already been removed because of management fisheries during the previous winter.

Van Eerden (1995) and by Trauttmansdorff & Wassermann (1995) as well as with Shags *Phalacrocorax aristotelis* (Johnstone *et al.* 1990). Duffy & Laurenson (1983) found in such experiments with Cape Cormorants *P. capensis* that a bird often produced two pellets a day, but that in all these cases only one contained fish remains. On this basis we assumed that a single pellet with fish remains represents the fish consumed during one day.

Some otoliths wear while being in the Cormorant's stomach. This is clear from pellet material and was shown in feeding trials in captivity with several cormorant species fed with fish of known length (Duffy & Laurenson 1983, Johnstone *et al.* 1990, Zijlstra & Van Eerden 1995). Wear causes an underestimation of fish-length, and consequently of fish-mass. Ideally, species-specific correction factors should be used in calculations. These can be obtained from either feeding trials or from comparison of the size of fish in the oesophagus with fish-length calculated from otoliths from the stomach of dead (drowned) birds (Piersma pers.

comm.). For Cormorants and the fish-species concerned here such correction factors have not been obtained yet. Piersma used the latter method in a study of Great Crested Grebes *Podiceps cristatus*. He concluded that the length of Smelt was underestimated with about 1 cm, while the estimates of Ruffe, Perch, Pikeperch and Roach were almost unaffected. In general, the wear in a Cormorants' stomach seems somewhat larger than in grebes, but the species specific differences caused by the characteristics of the otoliths are comparable. Marteijn & Dirksen (1991) also found that the amount of wear depended on shape and thickness of the otoliths. Based on their characteristics, otoliths of Smelt, Perch and Pikeperch are relatively vulnerable to wear, while Ruffe and cyprinid otoliths are less likely to wear substantially. Thus, length-frequency distributions of individuals eaten of Smelt, Perch and Pikeperch might be shifted a little towards smaller individuals. The effect on estimates of body mass, mainly lies in underestimation of Perch, because this is by far the most numerous in the diet of Cormorants of the three species mentioned. Because of the relatively low numbers taken, errors made for Smelt are of minor importance. When the proportion of Pikeperch is at its maximum in midwinter, larger individuals predominate in the pellets. As the small otoliths are most vulnerable, underestimation of this species seems to be of minor importance as well.

In the feeding trials mentioned above it was also found that part of the otoliths of fish eaten was not present in the pellets. The studies indicate differences according to fish and bird species. In our studies, however, the use of several other characteristic bone structures in addition to otoliths minimised the chance of fish not being found.

Daily intakes as calculated in our study do not seem to disagree with theoretic values of daily energy demands of Cormorants. The sample means of fish-mass estimated from the contents of the pellets varied between 146 and 699 g, the maximum in one pellet being 1223 g. Taking into account the variation in the caloric value of fish (varying roughly between 4.6 and 5.6 kJ/g fresh

mass throughout the year for the species eaten; Craig 1987, Buijse & Houthuijzen 1993), and using Aschoff & Pohl (1970) and Castro *et al.* (1989), these figures correspond to *c.* 1.0, 4.3 and 7.0 BMR respectively. As we are aware of the limitations of these energetic calculations, and the methodological problems in extrapolating from field data in which various sources of errors are not yet quantified, mentioning these BMR figures here is only meant to illustrate that the pellet data are in the right order of magnitude: In many studies, mean daily expenditure levels between 2 and 4 BMR have been reported (Kersten & Piersma 1987). Other authors using pellets report comparable daily intake figures (Voslamber 1988, Marteijn & Noordhuis 1991, Platteeuw *et al.* 1992).

Consumption and prey availability

In both seasons for which total food consumption by Cormorants was estimated, large cyprinids were underrepresented with respect to their relative abundance in lake Wolderwijd. The maximum size of Bream and Roach eaten in this study was 28 cm and 31 cm respectively, while maximum of 38 cm has been established in other studies (Veldkamp 1995a, Boudewijn & Dirksen own obs.). Therefore, the argument of fish being unavailable because of their size is only applying to part of the $\geq 1+$ Bream and Roach. Fish of intermediate sizes may still be less attractive because of e.g. relatively complicated handling or high swimming speed. In 1991/92 the large fish had been strongly reduced (Table 1), but still large Bream was underrepresented in the pellets. Apparently, the Cormorants strongly prefer the small, shoal-living size-classes of fish in the lakes. These are the fish caught when using the technique of mass flock fishing. Van Eerden & Voslamber (1995) argue that this technique is the Cormorant's answer to the deteriorated underwater visibility in shallow lakes caused by eutrophication. As this technique is especially useful for chasing shoals of fish in turbid water, the preference found here seems to be explained.

After correction of the stock estimate of Ruffe in lake Wolderwijd according to the catches

during fish removal, the consumption of small fish is far less in disagreement with the densities in which these occur than concluded earlier (Marteijn & Dirksen 1991). Nevertheless, percids were consumed in relatively higher proportions than cyprinids. Behavioural differences between fish-species may be important here. Suter (1991) gives several references for depth differences between species in periods with low temperatures. In lake Wolderwijd and lake Veluwemeer, in which the channel is 5 m at its deepest, segregation seems to be mainly horizontal. Especially young fish tend to gather in harbours along the lakes during winter (Witteveen+Bos 1990). Backx *et al.* (1992) present estimates of the densities of the different species and size classes according to habitat. In harbours small Roach and Bream (≈ 14 cm), and Ruffe were found to be present in almost equal densities. In the channel of the lake, however, the density of Ruffe was 2.5 times that of small Roach, while small Bream had an intermediate position. As the fish in harbours are less attractive to Cormorants than any shoals in the open water because of human disturbance, these data may explain the relatively high proportion of Ruffe in the pellets.

It is intriguing to try to explain the seasonal pattern in daily intake (Fig. 6). In August and September daily intake was at its lowest. In this period, many young and still inexperienced birds from colonies nearby can be found in the lake IJsselmeer region. Also, many of the 0+ fish attractive to the Cormorants later on are still very small in this period. Platteeuw *et al.* (1992) also found their lowest values (285 g) in August. By October, the young birds are more experienced and the fish have grown to reasonable sizes. Furthermore, birds probably need to put on reserves, either for migration or in anticipation for the winter. During November, December and January the daily intake was relatively low. In this period, the number of Cormorants present is lower as well: many birds prefer to leave the area after October. In fact, fish availability decreases in this period: many fish, especially the preferred small and shoal-living size classes, gather in the

harbours along the borders of the lakes (Backx *et al.* 1992). This is reflected also in relatively more large fish being taken, especially Pikeperch. In February and March daily intake increased again. By then, the birds are close to the start of the breeding season. Both sexes have reasons to put on extra body reserves: the females to produce eggs, the males for the period of settling and nest-building, in which they stay within the colony most of their time. It is striking that the frequency-distribution of pellet weights in the March-sample of all seasons shows a separate group of very high values, above 1 kg (see Fig. 5).

Cormorants and commercial fisheries

Commercial fisheries in the lakes still are of some economical value. Financially, the fishery on Eel with fykes is most important. In the period 1985-89 *c.* 6-13 kg Eel /ha/year was caught (pers. comm. Directorate of Fisheries). However, Cormorants do not catch Eel in relevant quantities in the non-breeding season, not even in August (Table 4). Thus, possible problems only occur during the breeding season, when numbers of Cormorants foraging in the lakes are usually small. Since Eel is caught by solitary fishing Cormorants, and this technique is observed only infrequently during this period, the problem is likely to be small.

Cyprinids, especially Roach and Bream, are also caught commercially, predominantly by seine fishing. The maximum amount of Roach which is allowed to be caught is 5 and 15 kg/ha for lake Wolderwijd and lake Veluwemeer respectively. Roach catches vary and amounted to *c.* 6-7 kg/ha/year in 1988-1989 (pers. comm. Directorate of Fisheries). Bearing in mind the tens of kg/ha of Roach probably still present in lake Veluwemeer and the catch of Cormorants, this cannot be regarded as a conflict situation. In lake Wolderwijd the effects of large-scale fish removal have largely overruled any possible effects of Cormorant consumption on commercial fisheries. Finally, in some years small amounts of Smelt are caught. Exploitation of percids is only permitted to anglers. The predation by Cormorants on pike

– an important species for water quality management – was almost nil.

Changes related to large-scale fish removal in lake Wolderwijd

In 1991/92 the only relevant change in Cormorant feeding conditions in lake Wolderwijd with respect to the 1989/90 season was the change in fish stock (Table 1). The transparency of the water was high in May and June, but had returned to its former level by July (Van Nes *et al.* 1992). Nevertheless, major changes occurred in the response of the Cormorants: (1) There was a shift towards feeding on smaller individuals within several fish-species; (2) the daily intake increased in autumn and winter but tended to decrease in spring; (3) due to (2) and the continued increase in bird-days spent in the area, the total fish consumption in lake Wolderwijd during the non-breeding season was about three times as high as in 1989/90. The fish removal clearly did not cause the birds to switch back to lake Veluwemeer for foraging.

Did the change in fish stock cause all the apparently beneficial effects for the Cormorants? Among the birds present in autumn are probably a lot of migrants from Denmark and the increase in numbers is probably related to the strong increase of the Danish breeding population. Apart from that, deteriorating feeding conditions in other areas (lake IJsselmeer) may have had an effect. However, neither of these factors explains the shift towards feeding on smaller fish and the increase in individual daily intake in 1991; these changes suggest a link to the fish removal. In winter 1990/91 most Cormorants had already left when the results of the removal gradually became evident, but on their return in autumn 1991 the situation had changed considerably (Table 1). Because many of the large fish were removed from lake Wolderwijd, the new cohort 0+ fish had good opportunities in 1991. Especially Ruffe, which apparently can act as pioneer-species in this kind of situations, did very well (Table 1), and the proportion of Ruffe in the pellets of Cormorants is exceptionally high in October and

November (Fig. 3). The combination of high proportions of small, shoaling fish and the still low and unchanged transparency made mass flock fishing seem very profitable. As a result flocks of several hundreds to a thousand Cormorants, chasing fish from the channel to the shallow parts of lake Wolderwijd, were regularly observed. This is reflected by the smaller size of prey, larger numbers of fish per pellet (Appendix 2) and significantly larger daily intake in autumn, as compared to the preceding winters. The decrease in daily intake in spring may have been caused by a decreased fish availability due to the heavy predation pressure in autumn and winter and the additional fish removal that was also carried out during these months.

The changes in Cormorant predation are generally favourable to the aims of the biological management plan. Cyprinids were the main goal of the fish removal efforts from the start, and Ruffe became a goal by the time it became clear how high the density of this bottom-feeder was. Especially the consumption of cyprinids and Ruffe by the Cormorants showed the highest increase in 1991-1992, as compared to the situation before fish removal (Table 4). Furthermore, the Cormorants hardly preyed on the Pike that had been released to enhance natural predation of small fish. Only the relatively high consumption of Perch and Pikeperch can be seen as negative, as the larger individuals of these species are predators like Pike. On the whole Cormorant predation seems to support the management programme. To the Cormorants on the other hand, the programme, should it prove successful, might be less advantageous. Increased transparency might change (depth) distribution patterns of fish and limit possibilities for mass flock fishing.

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SAMENVATTING

In de periode oktober 1989 - april 1992 is onderzoek uitgevoerd naar de voedsel生态学 van Aalscholvers in het Veluwemeer en het Wolderwijd. In deze meren fourageren vooral in het winterhalfjaar steeds meer Aalscholvers. De grootste aantallen worden meestal in oktober en november waargenomen; 1314 in oktober 1991.

Er waren twee redenen om het onderzoek uit te voeren: (1) het onderzoeken van eventuele schade aan de beroepvisserij en (2) het bepalen van het effect van vispredatie door de Aalscholvers op ecologische beheersmaatregelen ('actief biologisch beheer') die in het Wolderwijd zijn uitgevoerd en gericht zijn op het vergroten van de helderheid van het water. In dit kader is in de winter van 1990/91 het visbestand terug gebracht van 203 naar 46 kg/ha.

Voor de Aalscholvers was Pos, die voor de visserij van geen enkele betekenis is, de belangrijkste prooi-soort (60% op gewichtsbasis in 1991/92). Daarnaast kwamen Baars, Snoekbaars, Blankvoorn en Spiering in alle monsters voor. Paling, de belangrijkste vissoort die in de meren door beroepsvissers wordt gevangen, werd echter nauwelijks gegeten. De gemiddelde consumptie per dag varieerde van 146 tot 699 g per vogel, waarbij de hoogste waarden werden gevonden in oktober en maart. De totale consumptie werd in 1989/90 voor Veluwemeer en Wolderwijd samen geschat op 3.7 kg/ha (oktober-maart).

In 1991/92 foerageerde 80% in het Wolderwijd, waar in de periode sept-mrt naar schatting 12.5 kg/ha werd geconsumeerd, tegenover 2.1 kg/ha in het Veluwemeer. Gedurende deze laatste winter werd gemiddeld kleinere vis gegeten dan in 1989/90. Omdat een zeer groot deel van deze vis bestaat uit potentiële bodemwoelers (Pos, Blankvoorn, Brasem) lijkt het erop dat het biologisch beheersprogramma door de Aalscholvers wordt ondersteund.

In de discussie wordt ingegaan op de vraag of het grotere aandeel van kleine, in scholen voorkomende vis de mogelijkheden voor sociaal fourageren heeft vergroot, en zo de omstandigheden voor Aalscholvers op het Wolderwijd heeft verbeterd. Hiertegenover staat dat wanneer de lange termijn doelen van de biologische beheersmaatregelen worden bereikt, de fourageermogelijkheden voor Aalscholvers zullen verminderen.

Appendix 1. Summary of regression formulae used in computations of fish length and fish mass, for the samples from various months (see Methods).

species	fish length (<i>TL</i> , cm)	month	ref.
Eel	$16.438 \cdot OL - 1.968$	all	1
Bream	$20.64 \cdot PL + 2.689$	all	o.d.
Ide	see Roach I	all	
Roach I	$((PL + 0.0077)/1.05943) \cdot 14.75 + 2.495$	all	1 / o.d.
Roach II	$11.346 \cdot OL - 11.904$	all	2
Carp	$12.207 \cdot PL + 0.303$	all	o.d.
Pike	$8.702 \cdot OL - 15.3$	all	3
Smelt	$3.159 \cdot OL + 0.338$	all	4
Ruffe	$2.214 \cdot OL - 1.131$	all	4
Perch	$3.111 \cdot OL - 1.473$	all	4
Pikeperch	$4.064 \cdot OL - 2.720$	all	4
species	fish mass (<i>FM</i> , g)	month	ref.
Eel	$1.32 \cdot 10^{-7} \cdot (10 \cdot TL)^{3.41}$	all	1
Bream	$0.0114 \cdot (0.881995 \cdot TL - 0.569197)^{3.11974}$	8,9,10	6
	$0.0090 \cdot (0.881995 \cdot TL - 0.569197)^{3.16675}$	11	5
	$0.0105 \cdot (0.881995 \cdot TL - 0.569197)^{3.12815}$	12	5
	$0.0140 \cdot (0.881995 \cdot TL - 0.569197)^{3.05172}$	1,2	5
	$0.0090 \cdot (0.881995 \cdot TL - 0.569197)^{3.16994}$	3	5
Ide	$0.0035 \cdot TL^{3.35}$	all	7
Carp	$0.016739 \cdot TL^{2.987}$	all	o.d.
Roach, 0+	$0.0127 \cdot (0.911126 \cdot TL - 0.450032)^{3.03001}$	8,9,10	6
Roach, ≥1+	$0.0091 \cdot (0.911126 \cdot TL - 0.450032)^{3.21763}$	8,9,10	6
Roach	$0.0073 \cdot (0.911126 \cdot TL - 0.450032)^{3.26893}$	11	5
	$0.0103 \cdot (0.911126 \cdot TL - 0.450032)^{3.13682}$	12	5
	$0.0145 \cdot (0.911126 \cdot TL - 0.450032)^{2.99573}$	1,2	5
	$0.0110 \cdot (0.911126 \cdot TL - 0.450032)^{3.10888}$	3	5
Rudd	see Roach		
cyprinid spec.	for $OL < 2$ mm; see Roach		
	$1.5 \text{ mm} < OL < 2 \text{ mm}: 12 \text{ g}$	all	o.d.
	$OL \geq 1.5 \text{ mm}: 1.3 \text{ g}$	all	o.d.
Pike	$0.0477 \cdot OL^{4.686}$	all	3
Smelt	$0.0118 \cdot (0.9105 \cdot TL + 0.4740)^{2.82638}$	8,9,10,11	6
	$0.000000266 \cdot (10 \cdot TL)^{3.57}$	12,1,2,3	4
Ruffe, 0+	$0.0131 \cdot (0.9385 \cdot TL + 1.1876)^{3.05764}$	8,9,10	6
Ruffe, ≥1+	$0.0723 \cdot (0.9385 \cdot TL + 1.1876)^{2.34009}$	8,9,10	6
Ruffe	$0.0252 \cdot (0.9385 \cdot TL + 1.1876)^{2.77282}$	11	5
	$0.0205 \cdot (0.9385 \cdot TL + 1.1876)^{2.84414}$	12	5
	$0.0276 \cdot (0.9385 \cdot TL + 1.1876)^{2.70797}$	1,2	5
	$0.0240 \cdot (0.9385 \cdot TL + 1.1876)^{2.81033}$	3	5
Perch, 0+	$0.0144 \cdot (0.944443 \cdot TL + 0.037041)^{2.93612}$	8,9,10,11	6
Perch, ≥1+	$0.0089 \cdot (0.944443 \cdot TL + 0.037041)^{3.17472}$	8,9,10	6
	$0.0047 \cdot (0.944443 \cdot TL + 0.037041)^{3.38299}$	11	5
Perch	$0.0085 \cdot (0.944443 \cdot TL + 0.037041)^{3.21916}$	12	5
	$0.0080 \cdot (0.944443 \cdot TL + 0.037041)^{3.24030}$	1,2	5
	$0.0163 \cdot (0.944443 \cdot TL + 0.037041)^{2.94116}$	3	5
Pikeperch, 0+	$0.0056 \cdot (0.954065 \cdot TL - 0.291036)^{3.12130}$	all	6
Pikeperch, ≥1+	$0.0139 \cdot (0.954065 \cdot TL - 0.291036)^{2.87721}$	8,9,10,11,12	5
	$0.0044 \cdot (0.954065 \cdot TL - 0.291036)^{3.21397}$	1,2,3	5

TL: total fish length (cm); *OL*: otolith length (mm); *PL*: pharyngeal bone length (cm); *FM*: fish mass (g); Fork length - total length relations from Baarda & Kampen (1988), except for Smelt and Ruffe: A.D. Buijse (Agricultural Univ. Wageningen).

References: o.d. own data; 1 Voslamber 1988; 2 Platteeuw 1988; 3 Härkönen 1986; 4 Doombos 1979, 1980; 5 Backx *et al.* 1992; 6 Backx 1993; 7 W.G. Cazemier (RIVO-DLO).

Appendix 2. Prey composition (%) of Cormorants: (a) number of fish and (b) fish mass per sample, Lake Wolderwijd and Lake Veluwemeer, 1989-92.

(a)	oct '89	dec '89	feb '90	mar '90	oct '90	nov '90	dec '90	jan '91	feb '91	mar '91	aug '91	sep '91	oct '91	nov '91	jan '92	feb '92	mar '92
Eel			0.1								1.0						
Bream	0.2		0.1		0.7		3.6	0.5	0.4	0.1	0.3	0.1		0.1			
Carp													0.1				
Ide			0.1					0.3		0.1	0.3	0.1				0.1	
Roach	3.6		0.1	0.9	3.5	1.8	4.8	4.4	3.4	3.1	14.3	5.6	2.5	2.2	0.6	2.0	0.4
Rudd									0.1							0.2	
Cypr. spec.	12.6	3.3	2.4	1.2	17.4	42.2	51.8	29.6	30.4	18.5	15.6	7.1	19.1	19.2	11.4	16.4	20.8
Pike			0.1					0.2	0.1		0.3		0.0	0.1			
Smelt	1.3	4.5	1.2	2.1	3.9	0.2		3.4	1.2	7.1			2.5	0.5	3.8	3.0	1.6
Ruffe	48.1	79.0	78.9	77.3	41.7	33.4	8.4	40.2	42.8	54.5	12.3	38.8	66.4	61.0	73.3	53.0	55.4
Perch	32.9	3.7	15.4	18.3	28.5	12.8	19.3	16.6	15.2	15.3	35.2	45.1	8.3	13.9	9.8	24.1	21.5
Pikeperch	1.3	9.5	1.7	0.2	4.4	9.7	12.1	4.9	6.3	1.3	20.6	3.3	0.9	3.1	1.2	1.3	0.3
<i>n</i> fish	1030	243	1466	578	1474	569	83	592	933	1121	301	1231	4612	1671	1827	1058	1474
<i>n</i> fish/pellet	44.8	10.6	43.1	72.3	49.1	19.0	3.8	19.7	32.2	37.4	11.6	38.5	170.8	61.9	63.0	37.8	59.0
<i>n</i> (pellets with fish remains)	23	23	34	8	30	30	22	30	29	30	26	32	27	27	29	28	25
(b)	oct '89	dec '89	feb '90	mar '90	oct '90	nov '90	dec '90	jan '91	feb '91	mar '91	aug '91	sep '91	oct '91	nov '91	jan '92	feb '92	mar '92
Eel			1.3								2.6						
Bream	2.8		0.7		2.0		7.0	0.6	0.7	0.0	0.3	0.4		0.2			
Carp													0.1				
Ide			0.9					2.4		1.1	1.4	4.2				0.9	
Roach	12.6		0.8	8.3	7.8	2.8	4.0	4.3	7.5	7.4	32.5	22.2	5.9	5.3	2.3	8.0	4.6
Rudd									1.7							0.2	
Cypr. spec.	4.9	7.3	11.8	1.7	11.3	21.8	35.8	28.6	18.7	11.1	43.2	24.8	8.7	10.8	21.8	23.3	30.3
Pike			0.6					0.2	0.0		0.4		0.0	0.1			
Smelt	0.5	0.5	0.1	0.2	0.7	0.0		0.1	0.1	0.1			1.5	0.1	0.7	0.1	0.2
Ruffe	30.7	37.0	51.5	76.3	44.4	22.5	1.7	22.1	37.6	63.1	2.7	23.6	72.6	55.4	45.2	33.1	49.9
Perch	42.3	10.2	19.0	13.0	25.3	12.7	18.8	28.0	20.5	14.3	15.1	23.0	9.5	16.8	24.0	27.9	12.8
Pikeperch	6.1	45.1	13.5	0.5	8.5	40.1	32.7	13.7	13.2	2.9	1.7	1.9	1.7	11.3	5.9	6.4	2.2
total mass	10485	3371	13403	4741	15944	7470	5489	8266	11143	14019	4713	4671	18890	8205	11920	8201	9885
mean (g)	456	147	394	593	532	249	250	276	384	467	181	146	700	304	411	293	395
s.dev.	167	115	237	338	250	170	130	147	157	327	158	197	296	246	278	199	358