DIET OF CORMORANTS *Phalacrocorax carbo sinensis* AT WANNEPERVEEN, THE NETHERLANDS, WITH SPECIAL REFERENCE TO BREAM *Abramis brama*

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ABSTRACT Recent diet studies in a Cormorant colony in NW Overijssel, The Netherlands, reveal that analysis of regurgitated stomach contents and pellets have several limitations. Nonetheless, the best results of year-round diet studies are to be expected from pellet analysis, especially if a correction for wear in the stomach is applied. Since pellet production of Cormorants rearing young seems to be irregular or even stops, pellets possibly do not give an accurate impression of food eaten by these birds. Regurgitated stomach contents collected during the breeding season are likely to provide a better idea of the food of Cormorants rearing young. Roach, Bream and Pikeperch are the most important prey species, as shown by analysis of both pellets and regurgitates. Total fish consumption of the colony in 1991 was estimated at 245 ton by pellet analysis. Cyprinids made up *c.* 74% of that amount. The mass share of cyprinids in regurgitates in April-July 1991 was 86%. It is shown that at the study area the consumption of relatively large Bream (up to 31 cm) is far more important than has been suggested by most studies elsewhere. Consumption figures derived from this study suggest that Cormorants at Wanneperveen consumed at least *c.* 5-16% on mass basis from the available standing stock of Bream in the lakes surrounding the colony in 1991, emphasising on the larger individuals (> 200 mm).

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INTRODUCTION

Until the mid 1980s, the Cormorants *Phalacrocorax carbo sinensis* of Wanneperveen used to fish only in very small numbers in the shallow lakes surrounding the colony (Van Dobben 1952, Veldkamp 1985). In the past, main fishing areas were situated in lake IJsselmeer (Van Dobben 1952) and after the land reclamations of 1942 and 1957 in the lakes Zwarte Meer and Ketelmeer (Veldkamp 1986; Fig. 1). Coinciding with the recent recovery of the colony (Veldkamp 1991) social fishing of Cormorants in groups of up to 500 individuals occurs quite often in the lakes Beulakerwiede and Belterwiede and other smaller lakes near the colony. These shallow (1-2 m deep) eutrophic lakes which originate from peat digging, have always been subject to commercial fisheries for Eel *Anguilla anguilla* and Pikeperch *Stizostedion lucioperca*.

As a result of eutrophication processes, most lakes in The Netherlands have lost their submerged vegetations while at the same time the biomass of shoaling zooplanktivorous fish increased and the water got turbid (De Nie 1995). These events created favourable conditions for the social fishing of Cormorants (Van Eerden & Voslamber 1995). Most fish communities in the eutrophicated shallow lakes in The Netherlands have become dominated by Bream *Abramis brama*, which by its bottom foraging habits contributes substantially to water turbidity (Lammens 1987, Lammens *et al.* 1992). Besides man, Bream probably has only two predators that may have a substantial impact on its populations in Dutch lakes: Pikeperch and Cormorant. However, Bream over 15 cm fork length is hardly predated upon by Pikeperch (Lammens *et al.* 1992). In this paper the predation on Bream by the Cormorants of Wanneperveen will be discussed.

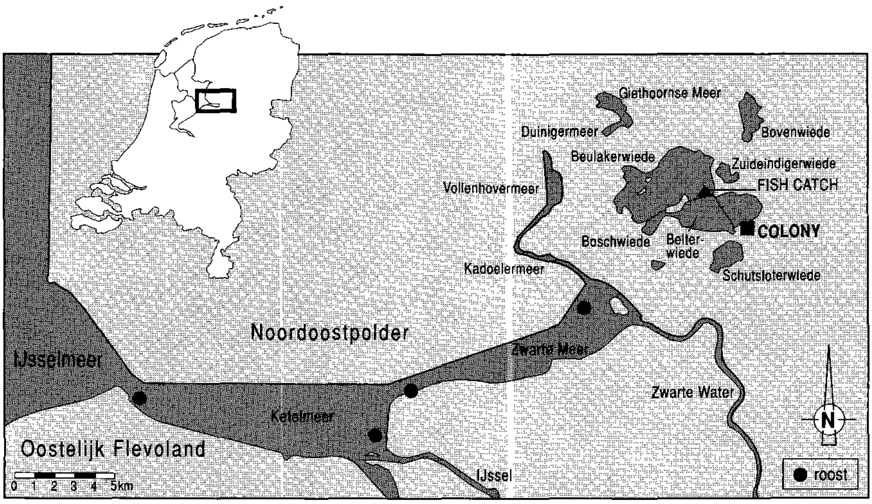

Fig. 1. The study area around Wanneperveen, NW Overijssel, showing the fishing areas of the Cormorants, the location of the colony and other roosts in the area. Also indicated is the site where 11 March 1991 local fishermen caught a sample of approximately 10 000 kg of Bream.

METHODS

Bird numbers

Counts were undertaken in a part of the colony visible from an observation hide in order to get an impression of trends in bird numbers throughout the year. During the breeding season these counts were made at the end of the morning when most birds had returned from the feeding areas. In the non-breeding season the counts were made at the end of the afternoon when all birds roosting at Wanneperveen were present. The number of breeding pairs was determined in the first half of May by counting the number of nests while walking slowly through the colony.

Diet studies

As a consequence of the visits to the colony during the breeding season, a minority of birds, adults as well as chicks, ejects partly digested and often completely undigested fish. In 1989-91 these ejected fish and fish remains were collected in the same way as by Van Dobben (1952) and De Boer (1972). Besides ejected fish, pellets were also collected during the entire period of Cormorant presence at Wanneperveen in 1991. With the help of a reference collection of otoliths, pharyngeal bones, chewing pads and other relevant fish remains which were prepared out of the ejected fish, it was possible to make a calculation of the fish consumption throughout the year.

Ejected fish Regurgitated fishes were collected 2-3 times a week during the breeding seasons 1989-91. This method of food sampling can probably only be used when a colony is well fed, which was the case in recent years at Wanneperveen (Veldkamp 1994). If regurgitates are collected soon after the returning of the birds from the fishing areas, often many completely undigested fish can be found. Partly digested fish usually have an undamaged body, but no head (Van Dobben 1952). Of these incomplete fishes the distance between the implant of the anal fin and tail fork was measured according to De Boer (1972). With help of completely undigested fish, which were also measured from snout to tail fork (in mm) and weighed, the regression formulae to reconstruct fish length and fish mass were calculated (Fig. 2 A, B).

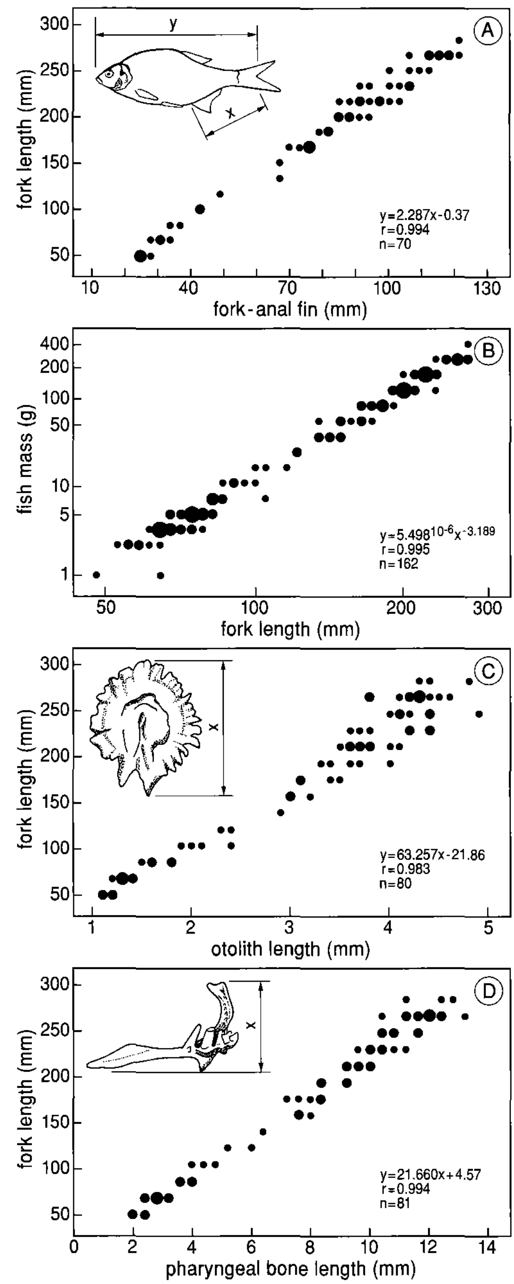

Fig. 2. Relationships among some body dimensions in Bream: (A) distance tail fork - implant anal fin and fork length, (B) fork length and fish mass, (C) otolith length and fork length, (D) pharyngeal bone length and fork length, according to linear regression formulae as indicated.

Pellets Cormorants produce mucus-covered pellets, as a rule probably once a day (Platteeuw 1988, Zijlstra & Van Eerden 1995, Trauttmansdorff & Wassermann 1995, own obs.), which contain remains of the fish eaten by the birds. In 1991 pellets were collected once a week, throughout the year. In the breeding season, collection frequency was even 2-3 times a week. Only complete and fresh pellets were analysed. Identifiable fish remains as otoliths (non cyprinids), jaws (Pikeperch) and chewing pads (cyprinids) (Veldkamp 1994) were sorted out and air-dried. Pharyngeal bones and otoliths (asterisci) of cyprinids were only sorted out when they obviously represented a greater number of fish then would be deduced from the number of chewing pads present in a pellet. All selected items were measured. If necessary, left and right pharyngeal bones were selected, the most numerous ones being measured using vernier callipers, taking the same measurement as used by Doornbos (1980). Fish remains were identified using a reference collection from intact ejected fish collected in the colony. The number of individuals represented in a pellet was defined as the highest total of the identifiable parts present. In the case of the Bream most individuals (92.5%) were recognised by chewing pads (see also Veldkamp 1995). The relationship between the length of chewing pads and fish length is given by Veldkamp (1995). Regression data on otoliths, pharyngeal bones, fish lengths and fish mass in Bream are given in Fig. 2.

Calculation of total consumption The total consumption per prey species in 1991 was calculated on a monthly basis. This was achieved by multiplying the estimated number of Cormorant days spent at Wanneperveen each month with the average fish mass per pellet of each species in the same month (Veldkamp 1994a).

Correction for wear Length-frequency distributions reconstructed from fish remains out of pellets often provide inaccurate estimates of the sizes of fish eaten (Johnstone *et al.* 1990). Fish remains from pellets are always to some extent affected by gastric juices. Using uncorrected measurements may therefore lead to an underestimation of the sizes of the fish eaten. For Bream a correction factor for the wear of chewing pads was calculated, by comparing a length-frequency distribution based on chewing pads from pellets with one of regurgitated fish from the same period.

RESULTS

Bird numbers

Since 1971 the number of breeding pairs in de colony of Wanneperveen has increased from *c.* 50 pairs to 940 pairs in 1991 (Veldkamp 1994). The colony is inhabited by Cormorants nearly througout the year (Fig. 3). Only in winter when ice covers the surrounding lakes, the colony is completely abandoned. In 1991, due to cold weather, arrival started late February. By the end of March most breeding birds were present. The noticeable increase in the number of birds in May coincided with many young birds leaving the nests and being included in the counts. As the breeding season ended (July, August), bird numbers tended to decrease a little. In September numbers rose again, reaching a maximum in October. The relatively high number of Cormo-

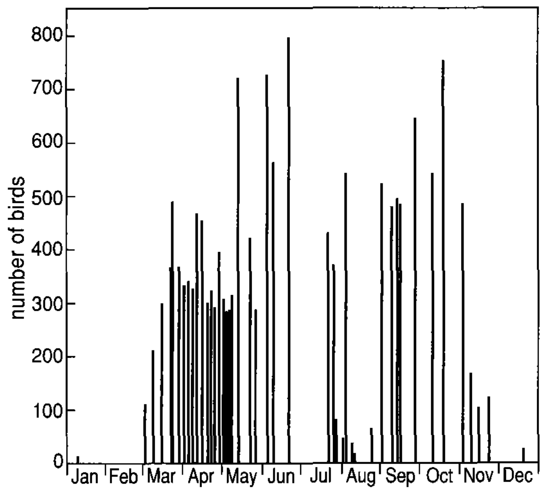

Fig. 3. Number of Cormorants counted in the colony of Wanneperveen in 1991. Data refer to a selected part of the colony (approximately 50% of the area), which is visible from an observation hide.

Table 1. Diet composition (in %) of Cormorants at Wanneperveen in April-July 1991, according to ejected fish and expressed by fish numbers (N) and fish mass (M). Total number and fish mass (kg) is given.

	April		May		June		July	
	N %	M %	N %	M %	N %	M %	N %	M %
Eel *Anguilla anguilla*	1.4	1.4	4.0	2.3	6.8	6.8	0.7	1.4
Bream *Abramis brama*	12.3	13.3	5.9	10.9	28.4	45.5	39.9	68.9
White Bream *Abramis bjoerkna*	0.0	0.0	8.7	14.2	14.8	20.9	0.0	0.0
Bleak *Alburnus alburnus*	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Roach *Rutilus rutilus*	73.6	68.2	69.6	58.0	37.5	13.2	33.8	20.9
Rudd *Scardinius erythrophthalmus*	0.0	0.0	0.0	0.0	0.3	0.4	0.0	0.0
Tench *Tinca tinca*	0.5	2.1	1.2	1.7	0.8	3.5	0.0	0.0
Pike *Esox lucius*	0.0	0.0	0.9	2.3	0.2	0.6	0.0	0.0
Smelt *Osmerus eperlanus*	0.0	0.0	1.4	0.0	1.4	0.1	12.8	1.6
Ruffe *Gymnocephalus cernuus*	5.2	0.3	4.2	0.3	5.9	0.6	8.1	2.0
Perch *Perca fluviatilis*	1.9	0.9	0.9	0.2	2.4	1.8	4.1	2.8
Pikeperch *Stizostedion lucioperca*	5.2	13.8	3.1	10.1	1.3	6.5	0.7	2.3
N	212	28.3	425	40.2	630	37.0	148	4.9

Table 2. Diet composition (in %) of Cormorants at Wanneperveen in 1991 according to pellet analysis (1087 pellets analysed) and expressed by fish numbers and fish mass. Total fish mass in kg.

in numbers	Jan	Feb	Mrt	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Eel *Anguilla anguilla*	0.0	-	0.1	0.1	1.0	1.0	3.3	1.0	0.0	0.0	0.1	0.0
Bream *Abramis brama*	2.1	-	2.8	2.4	4.8	7.1	8.0	4.2	1.2	2.7	2.7	1.2
White Bream *Abramis bjoerkna*	1.8	-	0.6	0.7	2.4	6.0	2.1	0.7	0.5	0.1	0.2	0.0
Carp *Cyprinus carpio*	0.0	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Ide *Leuciscus idus*	0.0	-	0.0	0.0	0.0	0.1	0.2	0.1	0.0	0.0	0.1	0.0
Roach *Rutilus rutilus*	22.6	-	12.0	19.4	39.7	36.0	55.0	46.1	58.6	26.6	34.3	3.0
Rudd *Scardinius erythrophthalmus*	0.6	-	0.1	0.2	0.4	0.3	0.0	0.0	0.0	0.0	0.2	0.0
Tench *Tinca tinca*	0.0	-	0.1	0.0	0.2	0.2	0.3	0.0	0.0	0.0	0.0	0.0
Pike *Esox lucius*	1.2	-	0.8	0.3	0.3	0.5	0.3	0.1	0.0	0.1	0.1	0.0
Smelt *Osmerus eperlanus*	0.0	-	48.2	35.8	18.8	25.0	1.5	8.3	13.5	47.2	28.5	78.1
Ruffe *Gymnocephalus cernuus*	15.9	-	24.9	27.6	14.9	9.0	16.7	29.7	21.5	17.3	21.0	13.7
Perch *Perca fluviatilis*	3.7	-	3.8	7.4	6.7	6.4	4.9	5.7	3.5	4.1	8.8	2.5
Pikeperch *Stizostedion lucioperca*	3.7	-	2.4	2.2	1.6	1.4	0.7	1.4	0.9	1.4	2.6	1.1
Undetermined cyprinid	48.3	-	4.3	3.7	9.2	7.2	7.2	2.7	0.2	0.4	1.5	0.3
Undetermined non-cyprinid	0.0	-	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
N	327	-	1923	4873	3596	3016	615	1631	3014	1969	2657	3317

in mass	Jan	Feb	Mrt	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Eel *Anguilla anguilla*	0.0	-	0.2	0.4	1.5	1.5	4.4	2.1	0.0	0.0	2.4	0.0
Bream *Abramis brama*	4.1	-	14.5	7.9	11.0	21.4	20.2	26.5	13.4	23.8	10.5	28.6
White Bream *Abramis bjoerkna*	1.8	-	2.0	1.4	5.1	12.9	2.5	3.0	1.4	0.5	2.6	0.5
Carp *Cyprinus carpio*	0.0	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ide *Leuciscus idus*	0.0	-	0.0	0.2	0.0	0.4	2.0	0.9	0.6	0.0	1.2	0.0
Roach *Rutilus rutilus*	16.3	-	28.6	46.9	53.9	32.8	44.6	46.2	62.6	38.6	42.6	22.2
Rudd *Scardinius erythrophthalmus*	2.7	-	0.0	0.3	0.1	0.7	0.0	0.0	0.0	0.0	0.2	0.0
Tench *Tinca tinca*	0.0	-	0.6	0.1	0.8	1.3	2.1	0.0	0.0	0.0	0.0	0.0
Pike *Esox lucius*	9.2	-	8.1	1.7	1.0	2.2	3.3	0.0	0.1	1.2	0.9	0.4
Smelt *Osmerus eperlanus*	0.0	-	2.9	1.2	0.4	1.0	0.1	0.3	1.4	3.0	1.8	14.8
Ruffe *Gymnocephalus cernuus*	3.1	-	10.8	8.2	3.3	1.8	2.0	4.8	10.0	7.7	8.4	12.6
Perch *Perca fluviatilis*	3.0	-	5.3	9.5	5.1	7.4	7.6	5.2	6.3	20.2	16.8	10.7
Pikeperch *Stizostedion lucioperca*	6.6	-	17.5	16.6	9.0	8.4	3.6	5.4	3.2	3.5	8.1	7.8
undetermined cyprinids	53.2	-	9.5	5.4	8.8	8.2	7.6	5.8	1.0	1.5	4.5	2.5
undetermined non-cyprinids	0.0	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
N	9.5	0.0	28.0	106.7	119.9	84.2	18.4	24.4	23.0	16.9	27.8	12.9

rants after the breeding season at Wanneperveen, suggests that fish stocks in the lakes surrounding the colony are far from depleted.

Diet composition

Ejected fish Between April-July 1991 1415 ejected fishes or fish parts were collected in the colony. According to mass Roach *Rutilus rutilus*,

Attempt of adult female Cormorant to swallow Perch *Perca fluviatilis* of super normal size, Oostvaardersplassen, 29 March 1991. (Photo B. Voslamber)

Bream, White Bream *Abramis bjoerkna* and Pikeperch were the most important species in the sample of regurgitated fish (Table 1).

Pellets Throughout 1991 1087 pellets containing fish remains were collected. In this material recognisable parts of 26 938 fish were found. Smelt *Osmerus eperlanus* was the most numerous prey, followed by Roach and Ruffe *Gymnocephalus cernuus*. Based on mass however, Roach was by far the most important food of the birds, dominating the diet almost all months (Table 2). Bream, Pikeperch and Perch were other important species. The first two species due to the often relatively big specimens taken.

Total consumption According to the analysis of pellets *c.* 74% of the total biomass consumed in 1991 consisted of cyprinids (Table 3). The most important species were Roach and Bream with a mass share of *c.* 46% and *c.* 17% respectively (see also Veldkamp 1994). The total consumption of the Wanneperveen colony in 1991 can be estimated at *c.* 245 ton. In the non-breeding season there were also other roosts in the area, at lakes Zwarte Meer and Ketelmeer (Fig. 1). Between July 1990 and April 1991 birds from these roosts withdrew *c.* 54 ton of fish from these two lakes (Platteeuw *et al.* 1992). Assuming that the consumption of these roosts for the whole of 1991 was about the same, the total consumption of Cormorants in the feeding area of the Wanneperveen colony (*c.* 7500 ha,) can be estimated at *c.* 300 ton, being *c.* 40 kg per ha.

Table 3. Calculated fish consumption of the Cormorants at Wanneperveen in 1991, according to pellet analysis without correction for wear. Species in order of importance.

Fish species	Consumption (x 1000 kg)
Roach *Rutilus rutilus*	113
Bream *Abramis brama*	42
Pikeperch *Stizostedion lucioperca*	22
Perch *Perca fluviatilis*	21
White Bream *Abramis bjoerkna*	13
Ruffe *Gymnocephalus cernuus*	12
Pike *Esox lucius*	5
Eel *Anguilla anguila*	4
Smelt *Osmerus eperlanus*	3
Tench *Tinca tinca*	2
Ide *Leuciscus idus*	1
Rudd *Scardinius erythrophthalmus*	1
unidentified cyprinids	6
total fish consuption	245

Predation on Bream

Seasons compared The length-frequency distributions of Bream eaten by Cormorants at Wanneperveen according to the sample of ejected fish during the breeding seasons 1989-91 (Fig. 4) show that in 1989 the ejected Bream were relatively large, having a mean mass of 121.9 g. In 1990 mean mass was 84.9 g, since more smaller 1+ (< 100 mm) specimen were eaten. Probably that same year class appeared in the ejected fish in 1991, as being 2+ and approximately 35 mm longer than in 1990. In 1991 at least four year classes could be found in the sample of ejected fish (mean mass 104.2 g). In all three years the number of Bream ≥ 200 mm was quite substantial. They represented about 70% of the biomass of Bream consumed (1989, 1990 and 1991 69.9%,

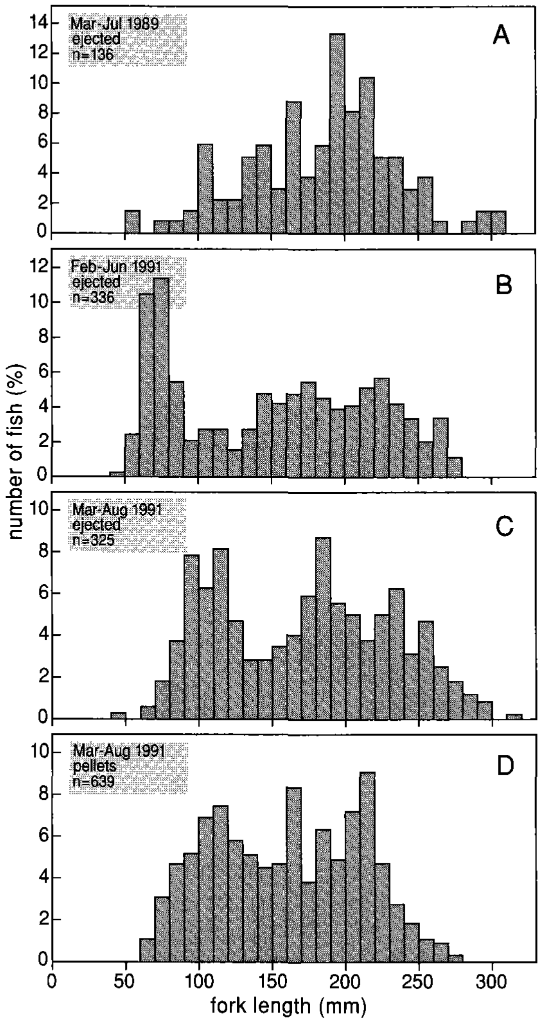

Fig. 4. Length-frequency distributions of Bream eaten by Cormorants at Wanneperveen during the breeding season: (A) March-July 1989, based on ejected fish, (B) February-June 1990, based on ejected fish, (C) March-August 1991, based on ejected fish, (D) March-August 1991, based on reconstruction from pellets, using only chewing pads without correction for wear. Distribution in March-August from ejected fish is significantly different from the distribution reconstructed from pellets in the same months (Kolmogorov-Smirnov two sample test, $p < 0.01$).

73.3% and 70.9% respectively). In 1989 the average ejected Bream was significantly longer than in 1990 (Kolmogorov-Smirnov two sample test, $p < 0.01$). The difference between 1989 and 1991 was not significant (K-S test, $p > 0.05$). The largest ejected Bream found at Wanneperveen in 1989-91 measured 313 mm (fork length)(Fig. 5).

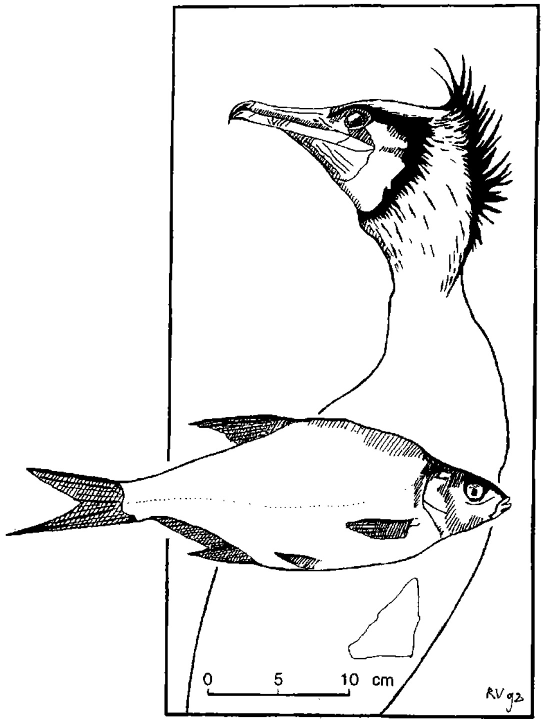

Fig. 5. To scale: Cormorant in breeding plumage with a Bream of about the maximum size that can be swallowed by the birds. (Drawing by author.)

Within-season variation As already shown in Table 2, Bream is consumed throughout the year, whenever Cormorants were present at Wanneperveen. Apart from November, the length-frequency distribution of Bream taken by Cormorants as reconstructed from fish remains in pellets in 1991 does not fluctuate very much in the course of the year (Fig. 6). A slight growth of the 1+ cohort is visible: from a mere 100 mm in March/April to 165 mm in late autumn. In November, when the number of birds present at Wanneperveen rapidly decreased, predominantly smaller Bream (< 150 mm) were eaten. The Bream taken

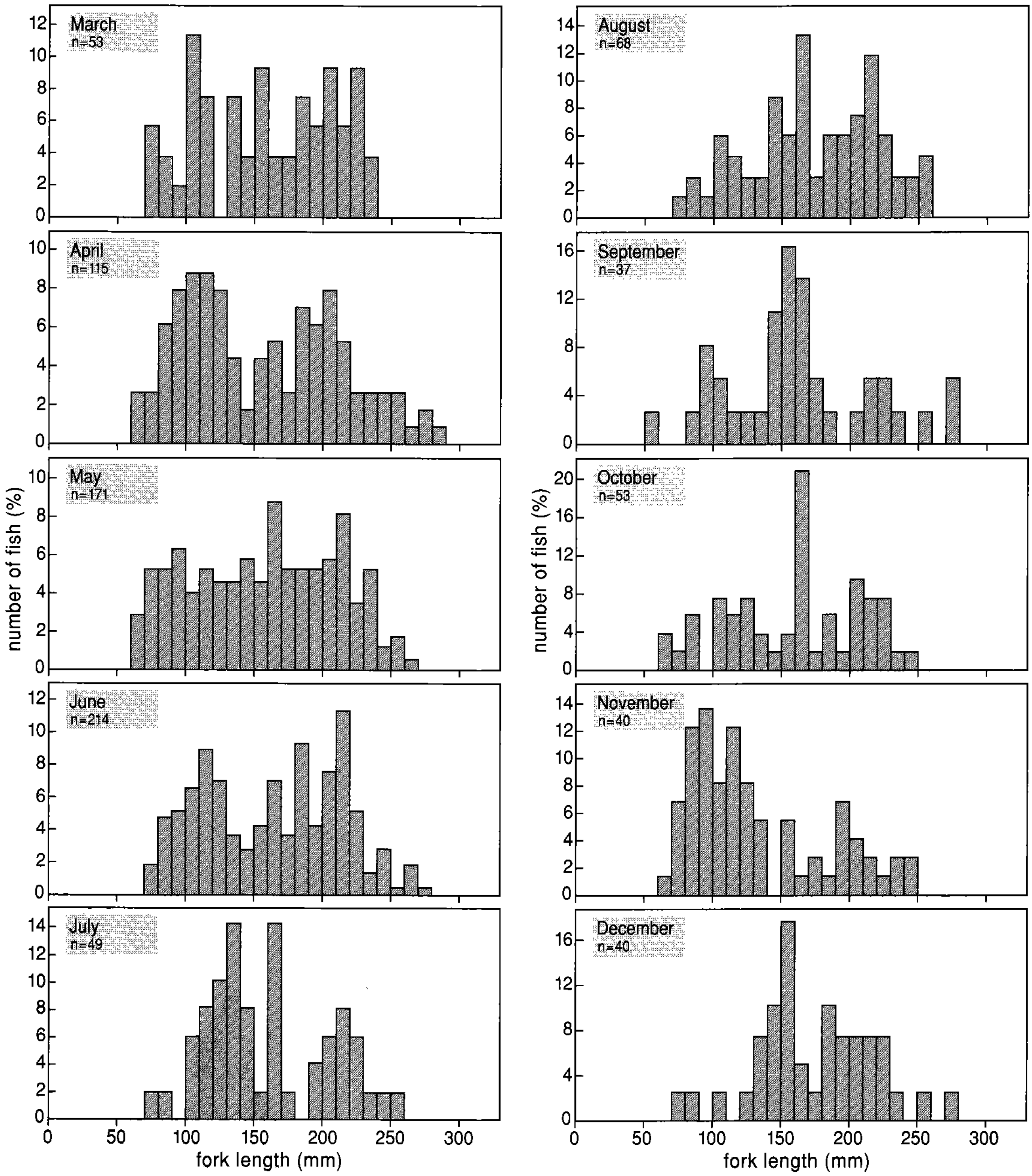

Fig. 6. Length-frequency distributions of Bream eaten by Cormorants of Wanneperveen throughout 1991. Data refer to reconstruction from pellet analysis and are not corrected for wear. Notice the appearance of 0+ Bream in the diet in November.

in November were significantly smaller than in the other months (K-S tests, September, $p < 0.01$, all other months $p < 0.001$). The availability of smaller 0+ Bream in November possibly increased as a result of the dying of emerse and (scarce) submerged vegetations, coinciding with a migration of larger Bream to the wintering sites. In December significantly more large Bream were caught than in most other months (K-S tests, March $p < 0.001$, April, June and July $p < 0.01$, May and September $p < 0.05$). However, with the exception of August and November, the numerical share of fish ≥ 200 mm was remarkably constant, ranging from 24 to 30%.

Estimation of wear Comparison of the length-frequency distribution of ejected fish collected during the 1991 breeding season with the one derived from chewing pads in pellets in the same period, showed significantly different distributions (Fig 4C/D, ejected fish/pellets, K-S test $p < 0.01$). The relatively strong length class of 160-169 mm in the pellets' sample approximately corresponds with the length class of 180-189 mm in the sample of ejected fish. Average chewing pad length in these classes measured 3.77 mm ($n = 53$) and 4.23 mm ($n = 28$) respectively. This difference in size of about 12% is probably due to a digestion effect. For the size classes 210-219 mm/230-239 mm (pellets/ejected fish) and 270-279 mm/310-319 mm) this figure was calculated at 8.6% and 12.3% respectively.

Thus, when using pellets, measurements of chewing pads have to be corrected at least with a factor 1.086, corresponding with an 8% size difference in masticatory plate length between ejected fish and pellet remains. This provides a better estimate of the length-frequency distribution of Bream eaten. This rather conservative figure was chosen to be sure not to overestimate the sizes of Bream taken by Cormorants.

DISCUSSION

Regurgitates *vs.* pellets

In a diet study of Shags *Phalacrocorax aristotelis* in Scotland, Harris & Wanless (1993) especially looked for pellets near nests with young but failed to find any. It was tentatively concluded that most of the pellets found had been produced by birds without chicks. In June and July it is often hard, or nearly impossible, to find fresh pellets in the Wanneperveen colony. Birds rearing young probably stop producing pellets because they have to hand over most or all fish caught to their young. Since chicks do not produce pellets (Van Dobben 1952, Trauttmansdorff & Wassermann 1995), and the parents have fewer fish remains to get rid of, it is likely that many pellets found in the period of young rearing are produced by birds without chicks. These birds may have a different diet than birds which do have chicks to feed.

In regurgitates, predominantly produced by breeding birds and their chicks, the mass share of Eel and Bream was larger as derived by pellet analysis, while the share of Ruffe and Perch was smaller (Table 4). An explanation for the differences can be that rather 'smooth' species like Eel and Bream are more easily regurgitated than spinyRuffe and Perch. On the other hand, since the vomiting of fish when disturbed should probably be interpreted as "emptying the stomach" before flying off, large and heavy fish are more likely to be regurgitated than smaller individuals. This is bound to cause considerable bias when

Table 4. Comparison of diet (in % of fish mass) according to ejected fish and pellets. Shown are mean values for Wanneperveen between April-July 1991.

Fish species	Ejected	Pellets
Eel *Anguilla anguila*	3.0	2.0
Bream *Abramis brama*	34.7	15.1
White Bream *Abramis bjoerkna*	8.8	5.5
Ide *Leuciscus idus*	0.0	0.2
Roach *Rutilus rutilus*	40.1	44.6
Rudd *Scardinius erythrophthalmus*	0.1	0.3
Tench *Tinca tinca*	1.8	1.1
Pike *Esox lucius*	0.7	2.1
Smelt *Osmerus eperlanus*	0.4	0.7
Ruffe *Gymnocephalus cernuus*	0.8	3.8
Perch *Perca fluviatilis*	1.4	7.4
Pikeperch *Stizostedion lucioperca*	8.2	9.4
undetermined cyprinids	0.0	7.5

comparing samples obtained by both methods. One cannot exclude either, that the differences found between regurgitates and pellets could also (partly) be due to a difference in diet between birds rearing young and birds without young (cf. Harris & Wanless 1993). The most serious drawback of the analysis of regurgitated fish, however, is the difficulty in making quantitative consumption estimates and the fact that ejected fish can only be found in the breeding season. Thus, in spite of its limitations, pellet analysis is probably the best method of assessing the food of Cormorants throughout the year and the only one that can support quantitative consumption estimates. Still, an underestimation of the sizes of fish eaten due to wear has to be taken for granted, unless one is able to correct for wear (cf. Dirksen *et al.* 1995).

Consumption of Bream

Recent publications on the food of the Cormorant in The Netherlands, all based on pellet analysis (Voslamber 1988, Boudewijn & Dirksen 1991, Boudewijn *et al.* 1991, Marteijn & Dirksen 1991, Marteijn & Noordhuis 1991, Platteeuw *et al.* 1992, Dirksen *et al.* 1995), seem to point out that Bream is rarely eaten by Cormorants. It is suggested that because of its high, laterally flattened body, Bream would be hard to swallow by the birds (Marteijn & Dirksen 1991, Marteijn & Noordhuis 1991, Suter 1991). However, some authors basing their work on regurgitates (Van Dobben 1952, De Boer 1972, Veldkamp 1991) found considerable amounts of Bream in the food of Cormorants in The Netherlands during the breeding season.

The results presented in this paper suggest that the Wanneperveen Cormorants do consume considerable amounts of Bream throughout the year and seem to have no trouble in handling specimens of > 200 mm fork length. Indeed, a comparison between a sample from a large catch of Bream (approximately 10 000 kg) in a marina of the Lake Beulakerwiede (see Fig. 1) on 11 March 1991 and the fish landed in the same period by the Wanneperveen Cormorants suggests that the birds even would prefer the larger individuals (Fig. 7). Mean fish mass in the human catch was 62.6 g, compared to 98.9 g and 100.3 g respectively for Bream taken by Cormorants in March 1991 and the entire year 1991. Among the Bream taken by the birds in March 1991, specimens of > 200 mm made up 71% of the consumed biomass of this species (70% for 1991 as a whole), while in the human catch the mass share of this size class was only 34%. This preference for larger Bream may be even stronger, since the human catch, made with a drag-net with a stretched mesh width of 20 mm, did not include Bream less than about 60 mm, which is impossible to catch with this gear type.

Ecological impact

The fish fauna of Dutch eutrophic lakes is increasingly dominated by Bream (Lammens 1987). Bream appear to be more successful than other closely related species like Roach and White Bream. Bream can exploit zooplankton very effectively, probably due to the structure of its pharyngeal sieve (Hoogenboezem 1991). In this way zooplankton becomes unable to reduce phytoplankton biomass and the water becomes turbid. Removal of large quantities of planktivorous (and benthivorous) fish, mainly Bream, has been applied in various lakes in The Netherlands with the aim of restoring water transparency (Grimm & Backx 1990, Van Donk *et al.* 1990). The data presented here on Cormorant predation on Bream allow an evaluation of the contribution this avian predator may make to biological management of eutrophic freshwater lakes.

In June 1992 trawl surveys were carried out in two lakes in the nature reserve De Wieden (Backx & Klinge 1992) in which the colony of Wanneperveen is situated. Total fish biomass during summer in the lakes Duiningermeer and Giethoornse Meer (Fig. 1) was estimated at 110-150 and 170-225 kg per ha repectively. If predation by the Cormorants of Wanneperveen is equally spread over the feeding grounds and Duiningermeer and Giethoornse Meer are representative for all the lakes surrounding the colony, it can be concluded that a substantial part (at least

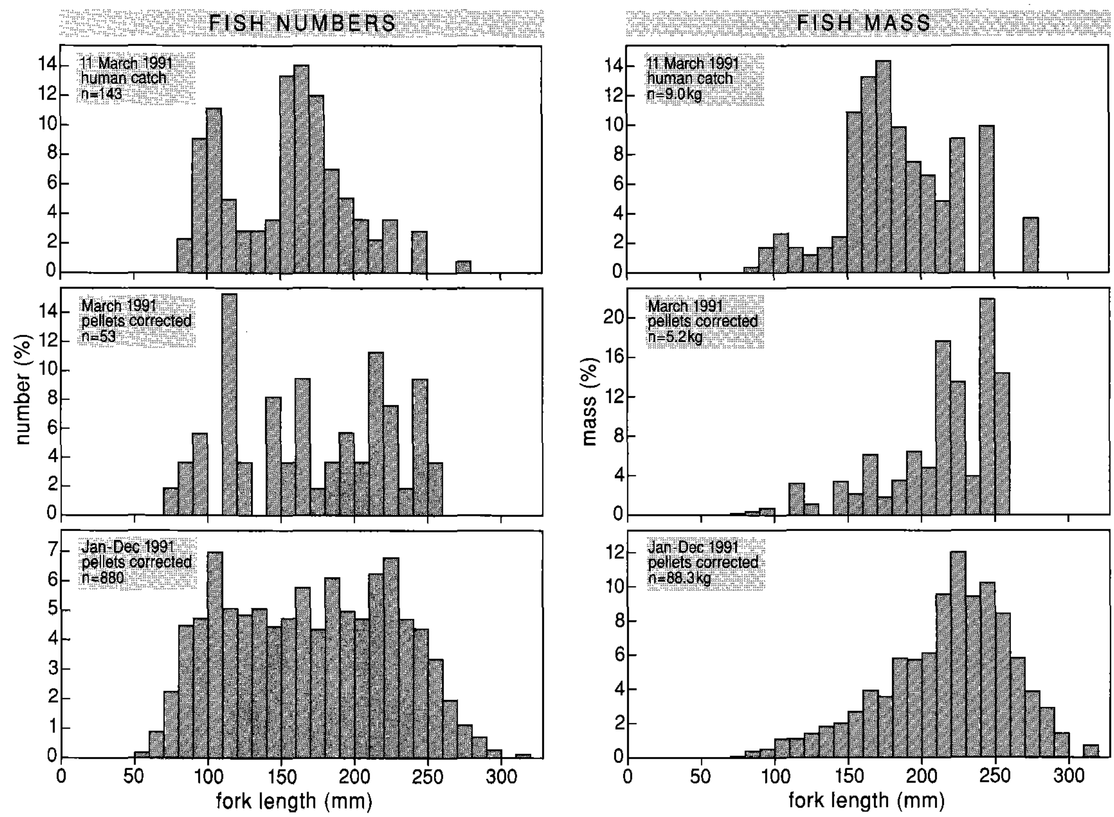

Fig. 7. Length-frequency distribution of Bream in a catch made by fishermen at lake Beulakerwiede (see Fig. 1), on 11 March 1991, compared to a length-frequency distribution as reconstructed from pellets of Cormorants at Wanneperveen in March 1991 and January-December 1991. Data are expressed in fish numbers as well as fish mass. Results from pellet analyses are corrected for wear.

15-30%) of the total fish biomass in these lakes was taken by the Cormorants. Predation pressure in the more nutritious lake Ketelmeer is probably lower since winter fish supply in that lake was valued at 86-427 kg per ha in 1989-91 (Bream > 250 mm total length not included; Platteeuw *et al.* 1992).

The proportion of Bream taken in relation to its stocks seems to be relatively small. The biomass of Bream in the Duinigermeer was estimated at *c.* 37 kg and in the Giethoornse Meer at *c.* 89-132 kg per ha in 1992 (Backx & Klinge 1992). Assuming that biomass figures in 1991 were about the same as estimated by the trawl surveys of 1992, at least *c.* 16% of the Bream biomass was taken away in the Duiningermeer and *c.* 5-7 % in the Giethoornse Meer (wear of fish remains from pellets not taken into account). Using the same assumptions, these figures were *c.* 33% and *c.* 65-72% respectively for the same lakes in the case of Roach, the main prey eaten by Cormorants from Wanneperveen. By taking away such quantities of zooplanktivorous fish, besides Bream and small Roach also small Perch, Ruffe and Smelt, the Cormorant may indeed have a positive influence on water quality by reducing the overexploitation of zooplankton (cf. Dirksen *et al.* 1995).

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SAMENVATTING

Een studie van het dieet van Aalscholvers in de kolonie van Wanneperveen (1991 940 broedparen) door het jaar heen toonde aan dat zowel het gebruik van uitgebraakte vis als dat van braakballen duidelijke tekortkomingen kent. De analyse van braakballen is de beste methode van dieetonderzoek gedurende het gehele jaar, zeker als er op de metingen van prooiresten uit braakballen een correctie voor de verterende werking van het maagzuur wordt toegepast.

Omdat de braakbalproductie tijdens het grootbrengen van jongen vermindert of zelfs stopt, geeft de analyse van braakballen waarschijnlijk geen goed beeld van de voeding van oudervogels en hun jongen. Hierover geeft de analyse van gedurende de jongentijd uitgebraakte maaginhouden wel informatie. Zowel uit de analyse van braakballen als uit de samenstelling van gedurende de jongentijd verzamelde braaksels komt naar voren dat Blankvoorn het voornaamste voedsel is, gevolgd door Brasem, Snoekbaars en Baars. De totale visconsumptie werd voor 1991 aan de hand van braakbalanalyses geschat op 245 ton. Karperachtigen maakten hiervan *c.* 74% uit. Het gewichtsaandeel van karperachtigen in uitgebraakte maaginhouden in april-juli 1991 was 86%.

Het meeste recente onderzoek naar voedsel van Aalscholvers veronderstelt dat Brasem (en met name de grotere exemplaren) niet of nauwelijks in het dieet voorkomt. De vogels uit Wanneperveen bleken echter, op basis van gewicht, wel een redelijke hoeveelheid Brasem te verorberen, vooral dankzij het feit dat de grotere exemplaren (> 200 mm) geprefereerd werden. In de meren van Noordwest-Overijssel is de predatiedruk op Brasem zo hoog dat in 1991 minimaal *c.* 5-16% van de voorradige biomassa werd geconsumeerd.