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The diet of the White-breasted Cormorant *Phalacrocorax carbo lucidus* along the Atlantic coast of West Africa

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The White-breasted Cormorant *Phalacrocorax carbo lucidus* occurs in Central, West, East and South Africa. The West African population breeds on the Cape Verde Islands and along the Atlantic coast from Mauritania to Guinea. The species forages in marine, brackish and fresh waters and is thought to be (almost) completely piscivorous. However, data on diet are poorly available and completely lacking for the West African population. We collected regurgitated pellets at three sites, in Mauritania (Island of Zira, Banc d'Arguin) and Senegal (Ilot aux Oiseaux, a small islet in the estuary of the Senegal River and Ile de la Madeleine near Dakar). On the basis of otoliths, 34 fish species belonging to 21 families were identified. There was great variation in the diet of the cormorants at the different sites, with Haemulidae and Batrachoididae being dominant on Ile de la Madeleine, Ariidae and Cynoglossidae on Ilot aux Oiseaux and Sparidae, Mugilidae and Batrachoididae on the Island of Zira. Most fish consumed were coastal species, many of which may also enter brackish or fresh waters. The cormorants mainly ate benthic and benthic-pelagic fish species varying in size between 10 and 20 cm. There was great variation in the number of otoliths per pellet at the different sites with a remarkably small number in the Zira sample. We investigated whether a small number of otoliths per pellet can be explained by the prey fish being larger or by the otoliths being more eroded. The latter might be an indication that part of the otoliths had been totally dissolved and thus disappeared from the samples. Neither fish size nor extent of wear could explain the small number of otoliths in the Zira sample. A comparison between artisanal fisheries catches and the diet of the cormorants showed hardly any overlap for the Senegalese sites. However, substantial overlap was found at the Banc d'Arguin in Mauritania. These differences can be explained by the high proportion of pelagic species caught in the Senegalese sites.

Key words: White-breasted Cormorant, *Phalacrocorax carbo lucidus*, diet composition, diet overlap, otoliths, West African coast

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The Great Cormorant *Phalacrocorax carbo* has often been regarded a pest species, as it is thought to take a substantial part of fish populations, which are also of interest to human fisheries. As a consequence, many studies have focussed on the feeding ecology of the two subspecies occurring in NW Europe: *P. c. carbo* and *P. c. sinensis* (e.g. van Dobben 1952, Dirksen *et al.* 1995, Grémillet *et al.* 1995, Warke & Day 1995, Keller & Visser 1999, Boström *et al.* 2012). In many cases the impact of cormorants on fish populations is limited and

economic loss to fishing industry much smaller than often suggested (e.g. Macdonald 1987, Carss 1993). While several Great Cormorant populations were heavily persecuted in the past, the species has now a (partly) protected status in many countries, which resulted in a significant population increase (Debout *et al.* 1995, van Eerden & Gregersen 1995, Birdlife International 2004).

Another sub-species of the Great Cormorant, the White-breasted Cormorant *P. c. lucidus* occurs in



Central, West, East and South Africa. It is not globally threatened and listed as of least concern on the IUCN Red Data List 2007 (IUCN 2008). The West African population is concentrated along the Sahelian Upwelling Marine Ecoregion, which extends along the Atlantic coast from Morocco to Guinea. The size of the West African population is estimated at 35,000 individuals (Wetlands International 2006). The White-breasted Cormorant is no exception to the rule that it is accused of causing damage to local fishermen due to its feeding habits. West African artisanal fishing is indeed under pressure. This, however, very likely results from a rapid increase in the number of artisanal fishing vessels and increasing pressure from international fishing fleets employing industrial fishing methods (Kaczynski & Fluharty 2002, Atta-Mills *et al.* 2004, FAO 2005, Agnew *et al.* 2009). At present, nothing is known about the diet of the species along the West African coast. Given that the presumed food resource of the species is under pressure, we argue that obtaining knowledge of the diet of cormorants is necessary to monitor the potential impact of changes in fish populations.

Most publications on the diet of the White-breasted Cormorant refer to inland freshwater situations (Du Plessis 1957, Whitfield & Blaber 1979, Linn & Campbell 1992) and only very few studies deal with marine feeding individuals (Wilson & Wilson 1988). A diet study should ideally cover a number of sites in both fresh water and marine environments. Such a comparison of data obtained in different sites may provide insights into how specialised the species is. Diet diversity may help to predict the potential effects fluctuations in fish populations may have. If there is little variation in diet both within and between colonies, then a reduction of the main food resource may severely affect the species (Barrett *et al.* 1987, Monaghan *et al.* 1992, Croxall *et al.* 1999, Furness 2007). On the other hand, if individuals belonging to different sub-populations utilise different food resources, the species may be better able to cope with changes on the meta-population level.

We have investigated the diet of the White-breasted Cormorant as part of a monitoring study of colonial piscivorous coastal seabirds along the West African coast. We collected regurgitated pellets at three sites in Mauritania and Senegal. Pellets were analysed, and fish otoliths were extracted, which were then used for identification at the lowest possible taxonomic level. We will deal with: (1) diet composition, (2) diet overlap between sites and years, and (3) characteristics of the fish consumed (benthic versus pelagic and occurrence in different water types). Our analysis shows that there are striking differences in the mean number of otoliths

per pellet in samples collected at different sites. We therefore also deal with (4) the question why there is so much variation in the number of otoliths per pellet and test the hypothesis that this might be related to the size of the fish consumed and/or the extent of wear of the otoliths. Finally (5), we compare artisanal fisheries catches with the diet of the cormorants to investigate overlap between both.

MATERIAL AND METHODS

Study species

Knowledge about the ecology of Great Cormorants almost exclusively comes from studies on the subspecies *P. c. carbo*, which mainly occurs along the North Atlantic coast, and the subspecies *P. c. sinensis*, which occurs in mainland Europe and Asia. The African subspecies *P. c. lucidus*, which is considered a separate species by some authors (e.g. Sibley & Monroe 1990), is poorly studied. *P. c. carbo* and *P. c. sinensis* occur in both marine and fresh water, avoid deep water and rarely feed far offshore. Both subspecies nest in colonies and roost gregariously. The diet almost exclusively consists of fish, which is obtained during the day by diving from the surface to a depth of 3–9 m (Cramp & Simmons 1986). Cormorants are usually solitary feeders, but group feeding may occur as well (e.g. van Eerden & Voslamber 1995, Veldkamp 2000). Daily food intake may vary greatly but usually consist of ca. 400–500 g fish (Grémillet *et al.* 1995, Ridgway 2010).

Collection and analysis of pellets

On the Banc d'Arguin foraging cormorants are difficult to approach. Moreover, prey may be swallowed under water. As a consequence diet data had to be collected by indirect methods, in this case by analysis of regurgitated pellets. Cormorants normally produce one pellet per 24 hours (Zijlstra & van Eerden 1995), which contains the otoliths of the fish consumed during that period. We collected pellets from three locations (Figure 1), which differed markedly in geographical characteristics. (1) On 27 April 2004, 42 pellets were collected on a roosting site on the island of Zira, which is situated on the Banc d'Arguin, Mauritania. Zira is surrounded by large expanses of tidal flats with creeks and channels of varying depth. The cormorants have been seen foraging on tidal flats during high tide as well as in gullies. There are no fresh water bodies in the area. (2) On 25 April 2004 and 4 June 2005, 45 and 100 pellets, respectively, were collected on a roosting site on a small islet, Ilot aux Oiseaux, in the estuary of



Figure 1. Map of the Atlantic coast of Mauritania and Senegal showing locations (black dots) where pellets of White-breasted Cormorants were collected in the period 2001–2005.

the Senegal River. The foraging area of the cormorants of this roosting site is unknown. The most likely feeding grounds are the nearby ocean, in brackish and fresh water in the river and in freshwater bodies (river, flood plains, lakes and marshes) situated upstream along the river. (3) On 28 November 2001, 49 pellets were collected in a breeding colony with active nests on a rocky island of the National Park ‘Iles de la Madeleine’ situated 2.5 km west of Dakar, Senegal. The cormorants breeding on Ile de la Madeleine are assumed to find their food exclusively in the surrounding ocean as freshwater bodies providing feeding possibilities hardly exist within the foraging range of the species.

In all cases we only collected complete pellets with an intact mucous outside layer. Most pellets were fresh (i.e. regurgitated during the night before) but in some cases small numbers of relatively dry pellets were included as well. The latter are regarded to be not older than a few days as older pellets completely dry up in the West African climate. Pellets were kept either each in an individual plastic bag (Ile de la Madeleine) or together in one bag (Ilot aux Oiseaux and Zira). They were subsequently transferred to small bags made out of plankton netting (mesh size 0.3 mm, Scrynel PA 300/47) and soaked for 24 hours in hot water with washing powder. Samples were afterwards put in a washing machine and washed at 70°C (pre-wash and main washing program with washing powder, without centrifugation). Washed samples were dried and spread out on a black surface, after which otoliths were picked out with the naked eye and by using a 2× magnifying-glass. All samples were searched twice. In all cases, less than 10% of the total number of otoliths in a sample

were found in the second searching round, suggesting that a large proportion of all otoliths were found.

Otoliths were identified, using reference collections of VEDA Consultancy and the Royal Natural History Museum, Brussels, together with literature sources (Veen & Hoedemakers 2005, Nolf *et al.* 2009). Each fish has three pairs of otoliths; the sagittae, utriculi and lagaenae. We only used *sagittae* because these best show species specific characteristics, except for the family of Ariidae for which *utriculi* were used. Otoliths were identified and measured using a binocular microscope (Novex 4.5–65×). We also measured the extent to which otoliths of some species had been eroded due to stomach acids. Following Leopold *et al.* (1998) we distinguished the following wear classes: (1) otoliths that were apparently complete, and still had irregular perimeters and a clearly visible sulcus, (2) otoliths that were smooth, but still had some of the original perimeter structure and sulcus visible, (3) otoliths that were smooth, had no original perimeter structure and in which the sulcus had lost most structural properties, and (4) otoliths as described under 3, but in which size had no relationship any more with the original size. Pictures of wear classes as defined above are given in Veen *et al.* (2003). In order to quantify the impact of wear on otolith size we compared them with specimens from our reference collection and estimated the original length. We then divided estimated original length by the actual length of the worn otolith, which resulted in the following multiplication factors per wear class: 1.08 (wear class 1); 1.11 (wear class 2), 1.15 (wear class 3); 1.24 (wear class 4). We used these data as a correction factor for otoliths of *Pomadasys incisus* which were converted to fish length (total length *TL*) using the formula $TL = 2.17 \times \text{length otolith} + 0.96$. *Pomadasys incisus* appeared to be the only species for which a conversion formula was available (Veen *et al.* 2003).

In order to quantify differences in diet composition between the samples, we used the Schoener Index of Proportional Overlap, where values range from 0 (no overlap) to 1 (complete overlap; Schoener 1970). Overlap indices were calculated on the basis of the lowest taxonomic level of the fishes distinguished (families, genera or species). Otoliths occur in pairs and although we often found otoliths which unmistakably formed a pair, we also found single right or left specimens. Several authors have reconstructed total number of fish by summing paired and single otoliths. In our samples many otoliths were difficult to pair due to wear. Therefore, we decided to simply present ‘total number of otoliths’, which thus represents the maximum number of individuals.

To investigate why the mean number of otoliths per pellet differed greatly between sites, we tested whether samples were different with respect to otolith size and wear. We used linear models to test for statistical differences in otolith size, focussing on the wear class with highest sample sizes. Due to low sample sizes we excluded *Tilapia guineensis* from Ilot aux Oiseaux 2004. Normality of the data was assessed using Shapiro tests and graphical methods. Data were normally distributed with the exception of *Halobatrachus didactylus* on Ile de la Madeleine. We therefore validated the results of the location comparison of this species with a non-parametric Kolmogorov–Smirnov test. We tested if the sampling location significantly contributed to the model by comparing models with and without location. This is first done for the full model including all three locations and then for the different pairs of locations. All statistical analyses were performed in R 2.14 (R Development Core Team 2011).

RESULTS

Diet composition

Altogether we found 4804 otoliths and 1 unidentified crab in the samples (Appendix 1). All otoliths showed wear and some were broken. As a consequence it was not possible to identify them all at the species level. We identified 28 species belonging to 16 fish families. For 6 additional genera or families no species could be identified. This means that at least 34 species must have been present in our material. 2% of the otoliths could not be identified. Most numerous species were *Arius* spec (38%), *Brachydeuterus auritus* (26%) and *Cynoglossus* spec (12%).

A comparison of species composition between sites is hampered by the various taxonomic levels of identification of prey. We have therefore chosen for a compari-

Table 1. Overlap indices for diet samples of White-breasted Cormorants collected at three sites along the Atlantic coast of West Africa: IaO = Ilot aux Oiseaux (Senegal river estuary), Zira = Ile Zira (Banc d'Arguin), Mad = Ile de la Madeleine (Dakar). Calculations are based on the lowest taxa identified as given in Appendix 1.

Site and year	IaO 2004	IaO 2005	Zira 2004	Mad 2001
IaO 2004	1	0.86	0.12	0.05
IaO 2005		1	0.11	0.04
Zira 2004			1	0.20
Mad 2001				1

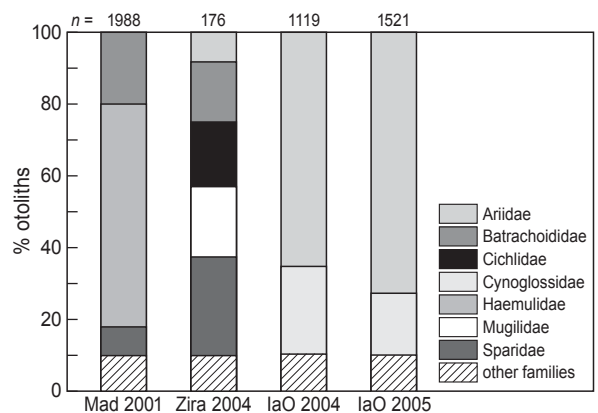


Figure 2. Diet composition (fish families) of White-breasted Cormorants in three sites along the Atlantic coast of West Africa, based on otoliths extracted from regurgitated pellets. Only fish families which occurred with more than 5% in a particular sample are depicted. Other families are lumped. The latter category includes a small proportion (0.8–3.2%) of otoliths which could not be identified. Mad = Ile de la Madeleine (near Dakar), Zira = Ile Zira (Banc d'Arguin) and IaO = Ilot aux Oiseaux (Senegal River estuary).

son at the family level, which allows us to include all data. Figure 2 gives for each site the percentage of fish families which occur in more than 5% of the pellets. Cormorants on Ile de la Madeleine mainly ate Haemulidae (62%) and Batrachoididae (20%). On Zira there was a predominance of Sparidae (30%), Mugilidae (23%), Cichlidae (17%) and Batrachoididae (19%). On Ilot aux Oiseaux, Ariidae (73% and 64%) and Cynoglossidae (18% and 24%) dominated in both years.

Diet overlap between years and sites

Diet overlap calculations were made on the lowest level of the taxa identified (Appendix 1, column 2) and are shown in Table 1. There was considerable overlap (0.86) between the two years in which samples were taken on Ilot aux Oiseaux. Overlap was small (0.20) between Ile de la Madeleine and Zira, and virtually absent between Ilot aux Oiseaux and Ile de la Madeleine and Zira (all between 0.04 and 0.12). It thus appears that the diet composition of the samples taken in consecutive years in the same site (Ilot aux Oiseaux) were very similar, whereas samples taken from different sites differed to a large extent.

Prey characteristics

Little is known about the feeding areas connected with the locations where the pellets were collected. However, the ecology of the fish species eaten may provide information about the cormorants' foraging

habitat. To this end we compared ecological information of the fish species (www.fishbase.org, Lloris & Rucabado 1998) with the diets at the three different sites. It appeared that the cormorants mainly ate coastal species, many of which may enter shallow waters, estuaries and lagoons. For each fish species we listed: (1) whether it occurs in marine (M), brackish (B) or fresh water (F) and (2) whether its occurrence in the water column can be characterized as pelagic (P), benthic-pelagic (BP) or benthic B (Appendix 1). We then calculated for each site the proportion of fish in relation to the habitat variables (Table 2). All fish eaten occurred in marine water, but the majority may also be found in brackish (MB 45%) or in brackish and fresh water (MBF 42%). Fish species that may also occur in fresh water (MBF) were especially abundant in the samples of Ilot aux Oiseaux, suggesting that cormorants from this site were foraging in all water types.

Cormorants rarely ate pelagic fish, but almost exclusively bottom-living species (99% of total, benthic and benthic-pelagic species taken together). The proportion of benthic and benthic-pelagic species was roughly the same at all sites.

Number of otoliths per pellet and otolith wear

The number of otoliths per pellet varied greatly between samples (range 4.2–40.6, mean 20.4, Appendix 1), with lowest mean number for Zira. Small numbers of otoliths per pellet can be explained by prey being larger or by the otoliths being more eroded. The latter might indicate that some otoliths may have been totally dissolved resulting in an underestimated number of prey. We therefore measured otolith size (as a measure of fish size) and extent of otolith wear of *Arius spec*, *Halobatrachus didactylus* and *Tilapia guineensis* and made a within-species comparison between

Table 2. Proportion of fish eaten by White-breasted Cormorants in relation to water type (combinations of M = marine, B = brackish, F = fresh) and occurrence in water column (P = pelagic, BP = benthic-pelagic and B = benthic), in three sites along the Atlantic coast of West Africa. N-values refer to the number of otoliths identified. Habitat data from fishbase.org., and Lloris & Rucabado (1998).

Site and year	Occurrence in water type (%)				Occurrence in water column (%)			
	M	MB	MBF	n	P	BP	B	n
IaO 2004	0.0	22.5	77.5	1074	0.3	81.5	18.2	1074
IaO 2005	0.0	29.6	70.4	1468	0.4	73.7	25.9	1474
Zira 2004	22.8	51.5	25.7	136	4.7	72.1	23.2	129
Mad 2001	30.1	69.1	0.8	1860	0.2	77.0	22.8	1868

Table 3. Extent of wear (for wear classes see methods) and size of otoliths (mean length \pm SE) of *Arius spec*, *Halobatrachus didactylus* and *Tilapia guineensis* in pellets of the White-breasted Cormorant collected in three sites along the Atlantic coast of West Africa.

Wear class	Mad 2001		IaO 2004		Zira 2004		IaO 2005	
	n	Length (mm)	n	Length (mm)	n	Length (mm)	n	Length (mm)
<i>Arius spec</i>								
1			203	5.74 \pm 0.04	13	10.57 \pm 0.25	157	6.03 \pm 0.04
2			40	4.76 \pm 0.12	1	9.10	43	5.29 \pm 0.06
3							4	4.85 \pm 0.16
<i>Halobatrachus didactylus</i>								
1	190	4.65 \pm 0.04			15	5.72 \pm 0.16		
2	75	4.25 \pm 0.05			6	4.53 \pm 0.29		
3	47	4.03 \pm 0.09			3	3.67 \pm 0.67		
4	19	3.21 \pm 0.11						
<i>Tilapia guineensis</i>								
1			5	6.26 \pm 0.19	1	6.50	10	6.62 \pm 0.14
2			2	5.75 \pm 0.45	9	5.21 \pm 0.40	12	5.74 \pm 0.18
3			1	5.00	5	5.06 \pm 0.37	8	4.54 \pm 0.25
4					6	4.18 \pm 0.08	10	3.76 \pm 0.23

the samples of Zira and the other sites. The results show that the size of *Arius spec* in wear class 1 differed significantly between locations in the full model ($F_{1,371} = 788.1$, $P < 0.001$). Sizes of *Arius spec* on Zira differed from those on Ilot aux Oiseaux in both 2004 and 2005 ($F_{1,214} = 713.9$, $P < 0.001$ and $F_{1,168} = 869.7$, $P < 0.001$, respectively) and between both years on Ilot aux Oiseaux ($F_{1,358} = 22.6$, $P < 0.001$), although mean values were very similar (see Table 3).

Size of *Halobatrachus didactylus* of wear class 1 differed significantly between Zira and Ile de la Madeleine (Kolmogorov–Smirnov test: $D = 0.672$, $P < 0.001$). Variances did not differ between sites (Levene's test for homogeneity of variance (R 'car' package): $F_{1,203} = 0.1$, $P = 0.72$) and hence the difference found can be contributed to size differences.

The size of *Tilapia guineensis* of wear class 2 did not significantly differ between Zira and Ilot aux Oiseaux 2005 ($F_{1,19} = 1.7$, $P = 0.20$)

We used contingency tables to compare frequency of otoliths in different wear classes between locations for each of the three major fish species. No statistically significant differences were found (Table 4).

Size of fish

For African fish species data on the relationship between otolith size and fish size are only scarcely available. We only found such data for *Pomadasys incisus* (present in sample of Ile de la Madeleine). The results showed that the otoliths of this species belonged to fish of 9.5 to 20.2 cm (mean 16.2, SD 1.95). A more general comparison of otoliths and specimens in our reference collection with known fish length suggested that the majority of fish consumed by the cormorants varied in length between 10 and 20 cm.

Competition with artisanal fisheries

In order to investigate the extent to which the White-breasted Cormorant might compete for fish with artisanal fisheries, we investigated fisheries statistics

Table 4. Pairwise comparisons of wear class distributions between Zira, Ile de la Madeleine (Mad) and Ilot aux Oiseaux (IaO 2004 and 2005).

Fish species	Location	χ^2	df	P
<i>Arius spec</i>	Zira – IaO 2004	0.30	1	0.582
<i>Arius spec</i>	Zira – IaO 2005	1.96	2	0.375
<i>Halobatrachus didactylus</i>	Zira – Mad	1.58	3	0.664
<i>Tilapia guineensis</i>	Zira – IaO 2005	0.80	3	0.850

available for Senegal (DOPM 2002, 2005 and 2006, Ba *et al.* 2006) and Mauritania (PNBA 2009). We used data of fish landings for Dakar (2001), St. Louis (2004 and 2005) and the Banc d'Arguin (2004–2007), which are situated at short distance from the cormorant sites Ile de la Madeleine, Ilot aux Oiseaux and Zira, respectively. Appendix 2 shows a summary of the data collected. The fisheries data are given in weight (tonnes) whereas the data on diet composition of the cormorants refer to numbers, allowing only a general comparison between both data sets.

In Dakar and St. Louis large numbers of fishing vessels are involved in artisanal fisheries and total landings amount to ca. 50,000 tonnes per year, composed of some 100 species and species groups. At both sites *Sardinella aurita* and *S. maderensis* are by far the most common species comprising 52% (Dakar) and 82–85% (St Louis) of all catches. The cumulative percentage of the 10 most caught species made up 78% (Dakar) to 93–94% (St. Louis) of total landings. Fish species which made up more than 5% of the diet of the cormorants on Ile de la Madeleine and Ilot aux Oiseaux were all different from the top-10 species landed at the fish auctions in Dakar and St. Louis. An exception were the Ariidae at Ilot aux Oiseaux, but this family only made up 0.80 to 0.83% of the landings at the St. Louis fish auction. So, for both Senegalese sites there seems to be very little overlap between the catches of artisanal fisheries and the diet of the White-breasted Cormorant.

The fisheries data for the Banc d'Arguin refer to the catches of the Imraguen people who live in the national park and have exclusive fishing rights in the area. Catches are much smaller than in the Senegalese sites and information available is far less detailed. In many cases several species are lumped into broad categories. An important part of the catches, e.g. the Ariidae (23%), Mugilidae (19%, *Mugil cephalus*), Cichlidae (7%) and Sparidae (3%), are all present among the species which make up more than five per cent of the diet of the cormorants on Zira. At the Banc d'Arguin there appears to be substantial overlap between the catches of artisanal fisheries and the diet of the cormorants.

DISCUSSION

We found that the diet of the White-breasted Cormorant varied greatly between sites with a few fish species being dominant in each site. Most fish species consumed were coastal species, many of which may

also enter brackish and fresh waters. Nearly all prey fish were benthic or benthic-pelagic species varying in size between 10 and 20 cm.

Sampling

When different methods of determining diet in piscivorous seabirds are compared, pellet analysis often comes out as being of questionable accuracy (Duffy & Laurenson 1983, Barrett *et al.* 2007). Fragile otoliths may break and, together with small ones, easily be overlooked. Moreover, otoliths extracted from pellets nearly always show extensive wear and small and thin specimens may have been totally dissolved because of the acid environment of the bird's stomach. Finally, it has been suggested that part of the otoliths may end up in the faeces instead of the pellets, as has been shown for terns by Veen *et al.* (2003). In a feeding experiment with captive cormorants Zijlstra & van Eerden (1995) found that the proportion of otoliths recovered varied from 0–83.5%, depending on the species and size of the fish, due to differences in detectability of the otoliths. Johnstone *et al.* (1990) obtained similar results when feeding shags *Phalacrocorax aristoteles* with marine fish. In contrast to the study on terns, Zijlstra & van Eerden (1995) found only a negligible number of otoliths in the cormorants' faeces (0.1%), which was also the case in a study by Leopold *et al.* (pers. comm.).

The wear of an otolith as a result of the acid gastric environment of a bird is not a constant factor, but depends on its size, shape and composition, as well as the conditions in the predator's stomach such as the degree of acidity and the time the otolith is ingested (Jobling & Breiby 1986). Duffy & Laurenson (1983) mention that the degree of wear also depends on the calcium demands of a bird and Harris & Wanless (1993) suggest that adult shags with young lower or stop pellet production, which probably means that the otoliths are completely digested.

The extremely poor recovery of otoliths in experiments with captive birds contrasts with several field studies showing that daily fish intake calculated on the basis of pellet analysis matches quite well with the energetic demands of the birds (Voslamber 1988 and Dirksen *et al.* 1995 in Zijlstra & van Eerden 1995). This suggests that experimental results might be importantly influenced by stress, which is known to increase calcium secretion and, consequently, causes an increasing calcium demand. The latter results in the increased production of acid gastric juices (Brooks 1967). Zijlstra & van Eerden (1995), when discussing their experiments, state that stress is the only reasonable explanation for the small number of otoliths recovered in their

study and conclude that it is unrealistic to compare the results obtained on birds in captivity and those under free-living conditions.

In this study we found considerable wear of otoliths, which was especially prominent in thin specimens such as those of *Cynoglossus spec.*, Cichlidae, Mugilidae and Serranidae. We also found broken otoliths, especially among the Clupeidae, Cichlidae and smaller sized Mugilidae. In a number of cases this clearly hampered species identification. However, we found very few otoliths which were close to being completely dissolved, except for a few *Cynoglossus spec.* The extent of wear observed, in combination with the presence of several small and fragile otoliths in our samples, suggests that no substantial numbers of otoliths were dissolved.

Zijlstra & van Eerden (1995) found that their experimental birds produced one pellet per day, which contained undigested remains from only the day before. Several authors come to similar conclusions (Platteeuw 1988, Dirksen *et al.* 1995, Veldkamp 1995) although variation in pellet production has been observed as well (Carss 1997), especially in relation to breeding. Adults feeding chicks may stop pellet production (Harris & Wanless 1993) and there are indications that chicks only start producing pellets when about two months old, while it takes about a year until pellet production reaches a level of ca. 1 per day (Trautmannsdorff & Wassermann 1995). In many studies, the otolith content of one pellet has been used to calculate daily food intake in mass. We have refrained from making such calculations for the following reasons: (1) separate pellets were only collected on Ile de la Madeleine, (2) many otoliths showed extensive wear and, missing relevant reference material, we were in many cases not able to compensate for wear, (3) for most species identified in our samples, data for conversion of otolith size to fish mass were not available.

It is of special interest that we found great variation in the number of otoliths per pellet between the different sites with a maximum of 40.6 on Ile de la Madeleine and a minimum of 4.2 on Zira. This is remarkable, as one would expect a low number of otoliths in the pellets of Ile de la Madeleine, since these pellets came from a colony with active nests, a situation with presumed high calcium demands. If we assume that each pellet contains a day's meal, the small number of otoliths per pellet in the Zira sample could be explained if: (1) it is correlated with relatively large fish, (2) many otoliths have dissolved or excreted through faeces, or (3) birds were under-nourished. We tried to test the first two possibilities, which was done

through comparing a number of taxa in the Zira sample with similar taxa in the other samples. No differences were found with respect to the extent of wear, but we found that the otoliths of *Arius spec* and *Halobatrachus didactylus* were significantly larger in the Zira sample. Nevertheless, we think this alone cannot account for the small number of otoliths in the Zira sample, which was 3.5–9.5-fold lower than in the other samples. Moreover, the proportion of *Arius spec* in the Zira sample was small (4.4%), while this was the only species which was considerably larger. We therefore conclude that the size differences of prey items may explain part of the differences in number of otoliths per pellet. Other explanations which could not be explored are (1) that the Zira cormorants were undernourished or (2) were feeding on non-fish prey which leaves no traces.

Species composition

Available studies on Great Cormorant diet show that this species exploits a wide range of fish, apparently concentrating on a few locally dominant prey species, with diets varying considerably between locations and seasons (van Dobben 1952, Pearson 1968, Kirby *et al.* 1996, Leopold *et al.* 1998, Radhakrishnan *et al.* 2010). These data fit with our finding that 34 fish species were taken, with only a few being dominant (*Arius spec*, *Cynoglossus spec.* and *Brachydeuterus auritus*), and with major differences between sites. At Zira and Ile de la Madeleine prey can only be taken from the ocean. At Ilot aux Oiseaux, however, the cormorants seem to exploit feeding opportunities in marine, brackish and fresh waters. Unfortunately, no data on fish availability are present to compare the diet of the cormorants with local fish availability.

All cormorant studies from marine and brackish areas emphasize a predominance of bottom-living fish in the diet, especially flatfish, *Pleuronectiformes* (e.g. Kirby *et al.* 1996, Leopold *et al.* 1998,). Moreover, it is stated that most fish vary in length between 15 and 20 cm (Marquiss & Carss 1994 in Kirby *et al.* 1996), although there are exceptions as shown by Leopold *et al.* (1998). This, again, fits with our data showing 99% of the diet to be composed of benthic and benthopelagic prey, usually varying in size between 10 and 20 cm.

Competition with artisanal fisheries

A comparison of catches of artisanal fisheries and fish consumed by the cormorants in Senegal and Mauritania is difficult, because the data available are expressed in weight (tonnes) and number of individuals, respectively. In the Senegalese sites there is hardly any species overlap between catches of artisanal fish-

eries and those of the cormorants. This can to a large extent be explained by artisanal fisheries predominantly targeting pelagic fish species of the families of the Clupeidae, Carangidae and Scombridae, whereas the cormorants almost exclusively take benthic fish species. In Senegal, sardinels (*Sardinella aurita* and *Sardinella maderensis*) alone made up between 57% and 85% of the yearly landings at the fish auctions of Dakar and St. Louis. Therefore, taking into account that our comparison is a very general one, competition for food between artisanal fisheries and White-breasted Cormorants seems to be low in Senegal.

The data obtained for the Banc d'Arguin, Mauritania, point in another direction. A variety of fish species important for artisanal fisheries is also targeted by the cormorants. So, competition might be substantial in this site. However, in this respect it is important to stress that the Banc d'Arguin covers a large area, in which fishing activities are rather limited and well regulated. The park is extremely rich in fish, which means that it is unlikely that the coexistence of artisanal fishing at its current scale and a flourishing cormorant population poses a problem in either direction.

White-breasted Cormorants are opportunistic feeders in a marine environment, which is extremely rich in fish. Our cormorant data show that diet composition was markedly different between sites, so the species is able to easily adapt to a changing availability of fish species. As far as competition with fisheries is concerned, it should be stressed that our comparisons are of a very general nature. White-breasted Cormorants are usually concentrated in certain sites, with thousands of individuals being present in a restricted area during breeding ((Banc d'Arguin > 3000 breeding pairs (Hafner *et al.* 1999); Ilot aux Oiseaux max. 3840 breeding pairs in neighbouring Djoudj National Park (Rodwell *et al.* 1996); Ile de la Madeleine 200–300 breeding pairs (Sauvage & Rodwell 1998)). This means that questions related to food competition should be studied at a more local scale and in far more detail than has been possible in this study.

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SAMENVATTING

De Afrikaanse ondersoort van de Aalscholver *Phalacrocorax carbo lucidus* broedt langs de Atlantische kust van West-Afrika van Mauritanie tot Guinee. Verondersteld wordt dat deze vogels uitsluitend vissen eten die in zout, brak en zoet water worden gevangen. Er zijn echter geen gegevens bekend over het voedsel van de West-Afrikaanse populatie. Wij onderzochten braakballen die in de volgende gebieden werden verzameld: (1) het eiland Zira in de Banc d'Arguin (Mauritanie), (2) Ilot aux Oiseaux, een klein eilandje in de monding van de Senegalrivier (Senegal) en (3) het eiland Ile de la Madeleine bij Dakar (Senegal). Op basis van otolieten (gehoorsteentjes) werden 34 vissoorten, behorend tot 21 families gevonden. Er waren grote verschillen in de voedselsamenstelling tussen de verschillende gebieden. Op Zira waren vertegenwoordigers van de visfamilies Sparidae, Mugilidae en Batrachoididae talrijk. Op Ilot aux Oiseaux vonden we vooral Ariidae en Cynoglossidae en op Ile de la Madeleine Haemulidae en Batrachoididae. De meeste gegeten vissen konden getypeerd worden als kustgebonden soorten, die in zout, maar vaak ook in brak en zoet water voorkomen. De aalscholvers aten vooral bodembewonende (benthische en benthopelagische) soorten. De prooilenkte bedroeg meestal 10–20 cm. Er waren grote verschillen in het gemiddeld aantal otolieten per braakbal per onderzocht gebied, met een opvallend gering aantal op Zira. Wij onderzochten of dit verklaard kan worden uit verschillen in prooigrootte of in de mate waarin de otolieten zijn aangetast door het maagzuur van de vogels. De aanwezigheid van sterk geërodeerde otolieten kan er namelijk op wijzen dat een deel van de otolieten volledig is opgelost. Beide onderzochte factoren konden het geringe aantal otolieten per braakbal in de monsters van Zira niet verklaren. Ten slotte is het voedsel van de aalscholvers in de verschillende onderzoekgebieden vergeleken met de plaatselijke vangsten van de traditionele visserij. In beide Senegalese gebieden was er vrijwel geen overlap tussen beide, maar in Mauritanie werd wel een aanzienlijke overlap geconstateerd.

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Appendix 1. Species composition and absolute numbers of otoliths of fish eaten by White-breasted Cormorants based on an analysis of pellets collected at three sites along the Atlantic coast of Mauritania and Senegal in the period 2001–2005. Codes used in the headings are as follows: Mad = Ile de la Madeleine (Dakar), IaO = Ilot aux Oiseaux (Senegal river estuary), Zira = Ile Zira (Banc d'Arguin); M = marine, B = brackish and F = fresh water; P = pelagic, BP = benthic-pelagic and B = Benthic. The data in the last two columns are derived from fishbase.org, and Lloris and Rucabado 1998.

Family name	Latin name	Mad 2001	Zira 2004	IaO 2004	IaO 2005	Total	M-B-F	P-BP-B
Ariidae	<i>Arius spec</i>		14	811	987	1812	MBF	BP
Batrachoididae	<i>Halobatrachus didactylus</i>	392	30			422	M	B
Bothidae	<i>Citharichthys stampflii</i>	1				1	MBF	B
	<i>Syacium micrurum</i>	1				1	M	B
	Bothidae	6				6		B
Carangidae	<i>Chloroscombrus chrysurus</i>		2			2	MB	P
	Carangidae	2			2	4		
Cichlidae	<i>Tilapia guineensis</i>		21	8	40	69	MBF	BP
	Cichlidae	30	10			40		
Clupeidae	<i>Sardinella maderensis</i>		4	1	6	11	MB	P
	Clupeidae	1				1		P
Cynoglossidae	<i>Cynoglossus spec</i>	9		196	375	580	MB	B
Gerreidae	<i>Eucinostomus melanopterus</i>	8				8	MBF	BP
Gobiidae	Gobiidae		1			1		BP
Haemulidae	<i>Brachydeuterus auritus</i>	1171		37	41	1249	MB	BP
	<i>Pomadasys incisus</i>	62				62	MB	BP
	<i>Pomadasys jubelini</i>	5		3	2	10	MBF	BP
	<i>Pomadasys spec</i>	1			4	5		
Hemiramphidae	Hemiramphidae	1				1		P
Moronidae	<i>Dicentrarchus punctatus</i>		8			8	MB	
Mugilidae	<i>Liza spec</i>		13			13		
	<i>Mugil bananensis</i>	1	10			11	MB	BP
	<i>Mugil capurrii</i>	15				15	MB	BP
	Mugilidae	17	12	32		61		
Polynemidae	<i>Galeoides decadactylus</i>	1				1	MB	BP
	<i>Pentanemus quinquarius</i>			2	6	8	MB	BP
Pristigasteridae	<i>Ilisha Africana</i>			2		2	MB	P
Sciaenidae	<i>Pseudotolithus elongatus</i>				1	1	MB	BP
	<i>Pseudotolithus senegalensis</i>				2	2	MB	BP
	<i>Pseudotolithus typus</i>			10	4	14	MBF	BP
	<i>Pteroscion peli</i>	2		4	1	7	MB	BP
	<i>Umbrina cirrosa</i>				3	3	MB	BP
Serranidae	<i>Cephalopis taeniops</i>	2				2	M	BP
	<i>Serranus cabrilla</i>	13				13	M	BP
	Serranidae	1				1		
Soleidae	<i>Synaptura lusitanica</i>	18				18	MB	B
	Soleidae				6	6		B
Sparidae	<i>Diplodus bellottii</i>	152	1			153	M	BP
	<i>Diplodus sargus</i>	4	43			47	MB	BP
	<i>Lithognathus mormyrus</i>	2	3			5	MB	BP
	Sparidae	3	2	4		9		
Sphyraenidae	<i>Sphyraena sphyraena</i>	1				1	M	P
Trachinidae	<i>Trachinus spec</i>				2	2		
Indeterminata		66	2	9	39	116		
Total		1988	176	1119	1521	4804		
Number of pellets		49	42	45	100	236		
Otoliths per pellet		40.6	4.2	24.9	15.2	20.4		

Appendix 2. Artisanal fisheries statistics for years and sites in which diet data on White-breasted Cormorants were collected. The data refer to all fish landings in 2001 in Dakar (near breeding colony on Ile de la Madeleine), in 2004–2007 on the Banc d'Arguin (area around roosting site on Zira) and in 2004 and 2005 in St. Louis (near roosting site Ilot aux Oiseaux). In addition to general data (upper part), the table gives the ten most abundant species or species groups as a proportion of total landings. The data are derived from DOPM (2002, 2005 and 2006), Senegal, and PNBA (2009), Mauritania. Local names were translated to species or species groups using fishbase.org, Vakily *et al.* (2002) and Lloris & Rucabado (1998).

	Dakar	Banc d'Arguin	St.Louis	St.Louis
Year	2001	2004–07	2004	2005
Number of vessels	2187	?	173	246
Number of fishermen	10–20000	?	1702	2415
Number of species (groups)	95	19	84	101
Total landings (tonnes)	33224	700	53788	49305
Local name	Family name	Species name		
Mâchoiron	Ariidae		23	0.80
Grande carangue	Carangidae	<i>Caranx hippos</i>	1.52	
Petite carangue	Carangidae	<i>Chloroscombrus chrysurus</i>		1.60
Chinchard jaune	Carangidae	<i>Decapterus rhonchus</i>	3.43	
Chinchard noir	Carangidae	<i>Trachurus trachurus</i>	3.52	0.53
Requins divers	Selachimorpha		13.5	
Toumvertel	Cichlidae		6.5	
Sardinelle ronde	Clupeidae	<i>Sardinella aurita</i>	44.62	58.34
Sardinelle plate	Clupeidae	<i>Sardinella maderensis</i>	12.65	24.39
Anchois	Engraulidae	<i>Engraulis encrasicolus</i>	3.04	
Requin dormeur	Ginglymostomatidae		2	
Carpe blanche	Haemulidae	<i>Pomadasys rogerii</i>		0.86
Pelon	Haemulidae	<i>Brachydeuterus auritus</i>		0.52
Mulet jaune	Mugilidae	<i>Mugil cephalus</i>	19	
Tassergal	Pomatomidae	<i>Pomatomus saltatrix</i>		1.39
Raie guitare	Rhinobatidae		2.3	0.99
Raies diverses	Batoidea		7	0.91
Maquereau espagnole	Scombridae	<i>Scomber japonicus</i>	4.43	2.50
Thonine (ravil)	Scombridae	<i>Euthynnus alletteratus</i>		1.81
Courbine	Sciaenidae	<i>Argyrosomus regius</i>	7	0.83
Mérou blanc	Serranidae	<i>Epinephelus aeneus</i>	1.28	
Badèche	Serranidae	<i>Epinephelus costae/fasciatus</i>	1.58	
Pageot	Sparidae	<i>Pagellus bellottii</i>	1.58	
Daurades	Sparidae		3.1	
Requins marteaux	Sphyrnidae		3.5	
Emissole	Triakidae			1.39
Total of top-10 species (%)			77.65	86.9
			93.72	92.60