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Diet of cormorants and the impact of cormorant predation on juvenile flatfish in the Dutch Wadden Sea

Mardik F. Leopold [a,*], Cindy J.G. van Damme [b], Henk W. van der Veer [b]

[a] *Institute for Forestry and Nature Research (IBN-DLO), P.O. Box 167, 1790 AD Den Burg, Texel, The Netherlands*
[b] *Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands*

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Abstract

Predation by great cormorants *Phalacrocorax carbo* on juvenile flatfish in the Dutch Wadden Sea was estimated from otoliths found in 182 regurgitated pellets. Pellets were collected at the main night roosts and in one colony, in late summer when cormorant numbers peak in the area. Otoliths of at least 24 different fish species were found, including both marine and freshwater species. Flatfish on average amounted to 73% of the fish found in numbers and contributed 79% by mass to the birds' diet. Among the flatfish species, 0-group fish were predominantly taken. Plaice *Pleuronectes platessa* was found most frequently (46% of all 0-group flatfish, $n = 6318$), followed by dab *Limanda limanda* (34%), flounder *Platichthys flesus* (19%) and sole *Solea solea* (1%). Total consumption by cormorants was estimated by multiplying the number of cormorant-days over summer (184 days) by the mean number of flatfish found in the pellets per sampling location, under the assumption that each pellet contained the remains of the fish eaten during 24 hours and that the diet was similar in all summer months. In total about 28.58 million flatfish were consumed over summer, 27.46 million of which were 0-group fish, including 12.55 million 0-group plaice, 9.45 million dab, 5.17 million flounder and 0.29 million sole. These figures are underestimates, because some otoliths were clearly missing, and estimated average daily intake per cormorant on the basis of all otoliths found in the pellets (460 grams of fish) was only 70 to 90% of the theoretical daily food requirement. In 1992 and 1993 0-group flatfish abundance was very low and cormorant predation during the period July to September (92 days) accounted for 49.5% of the total stage mortality in 0-group plaice in 1992 and 27.3% in 1993. However, in normal years the impact of cormorant predation will be much lower.

Keywords: cormorant; *Phalacrocorax carbo*; flatfish; plaice; Wadden Sea; predation; otolith-wear; pellets; diet

1. Introduction

The coastal zones of the North Sea and the Wadden Sea are important nursery areas for several North Sea flatfish species, such as plaice *Pleuronectes platessa*, dab *Limanda limanda*, flounder *Platichthys flesus* and sole *Solea solea* (Zijlstra, 1972; Dankers et al., 1978; Van Beek et al., 1989; Bolle et al., 1994). Being abundant in the area, juvenile flatfish are included in the diets of a range of other animals. Larval plaice and flounder are preyed upon by coelenterates (Van der Veer, 1985), and just settled juveniles suffer predation by shrimps *Crangon crangon* and crabs *Carcinus meanas* (Van der Veer, 1986; Van der Veer and Bergman, 1987). With increasing flatfish size, other predators, such as fish, birds and seals become

* Corresponding author. E-mail: m.f.leopold@ibn.dlo.nl

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dominant (Macer, 1967; Edwards and Steele, 1968; Van der Veer, 1986). This sequence of predators appears to be a rather general pattern also operating in other coastal flatfish nurseries (Pihl, 1990; Van der Veer et al., 1990, 1997; Ellis and Gibson, 1995).

Studies on plaice and flounder suggest that year-class strength is already determined in the pelagic stages (Brander and Houghton, 1982; Van der Veer, 1986; Van der Veer et al., 1991). Later on, mortality inflicted by shrimps and crabs appears to be significant (Van der Veer, 1986; Van der Veer and Bergman, 1987; Pihl, 1990; Van der Veer et al., 1990, 1991) but only in a regulating way, dampening the interannual variability in year-class strength (Van der Veer, 1986; Van der Veer et al., 1990, 1991; Beverton and Iles, 1992). Beverton and Iles (1992) reviewed all available information on mortality of juvenile flatfish in European waters and concluded that in summer, after the period of predation by crustaceans significant mortality among juvenile flatfish still occurs. This suggests that the combined effect of predation by fish, birds and seals and fishery induced mortality by shrimping in the area (Berghahn et al., 1992; Berghahn and Purps, 1998) is important. Ellis and Gibson (1995) concluded that once flatfishes had attained a size of 45 mm, they had outgrown the fish predators present in their area of study, Trallee Bay, Scotland. Assuming a similar situation for the Wadden Sea, this means that predation by birds and/or seals might be significant during the summer period, but no quantitative information exists on these sources of predation. This study aims to quantify the predation pressure by one of the main avian predators, the great cormorant *Phalacrocorax carbo*. Cormorants are large piscivores that, in high densities may be important predators of juvenile fish, particularly in enclosed water bodies (Mills, 1969; Barrett et al., 1990; Van Dam et al., 1995).

Previous research in Cornwall and in the Wadden Sea has shown that more than 40% of cormorant prey items consisted of juvenile flatfish (Steven, 1933; Van den Berg, 1993; Van Damme, 1994; Nehls and Gienapp, 1997). Most cormorants arrive in the Dutch Wadden Sea in April–May and they leave the area again in September–October. Cormorants breed in the Wadden Sea in increasing numbers (Leopold and Van den Berg, 1992; Camphuysen et al., 1995; Van Dijken, 1997) and birds from mainland colonies also use this area and the adjacent waters of the coastal North Sea in summer to feed and prepare for migration (Camphuysen and Leopold, 1994). After feeding, cormorants gather on night roosts, where they socialise, rest and regurgitate indigestible items of prey ingested previously. Regurgitated pellets were collected in five main roosts and one colony in August/September, when cormorants are most abundant in the Wadden Sea. Prey species were identified from otoliths and other hard parts in these pellets. For each fish species, otolith size was used to reconstruct the original prey size and mass. Based on these estimates, total predation on flatfish was calculated. These figures were compared with estimates of total juvenile flatfish abundance in the area, to demonstrate the importance of this source of predation.

2. Material and methods

2.1. Sampling

In the Dutch Wadden Sea two colonies and several important night roosts of cormorants were found in 1992 (Leopold and Van den Berg, 1992; Camphuysen et al., 1995). Pellets were collected in the oldest colony, De Hond, an artificial island in the Ems estuary, and the following night roosts: De Schorren, a protected saltmarsh and nature reserve on the eastern side of the island of Texel; Kooihoekschor, a similar, protected saltmarsh at the Balgzand, southwestern Wadden Sea; a breakwater in front of the sluice and harbour of Den Oever, southern Wadden Sea; Griend, a bird sanctuary in the central Dutch Wadden Sea and Boschplaat, a nature reserve on the island of Terschelling (Fig. 1). The average total number of cormorants present in the Wadden Sea was estimated from bird counts by SOVON (Joint Bird Research, Netherlands) and our own observations. These two sources of information were combined to get monthly estimates of cormorant numbers present in the Dutch Wadden Sea in 1992–1993.

Cormorant pellets were collected in the colony De Hond in September 1992 and on the night roosts in August 1993. Only complete and fresh pellets were taken. Twenty-five to 38 pellets were collected at each location and kept at −20°C. Pellets were always treated individually, except for Boschplaat, where 35

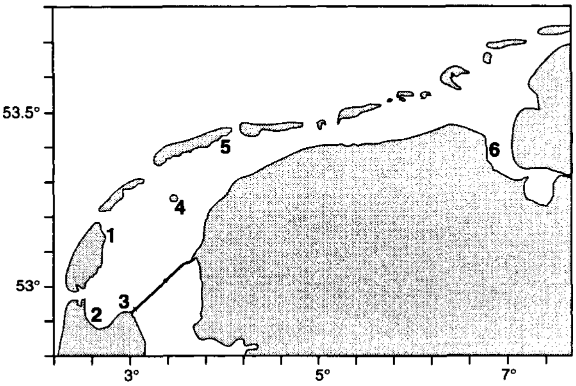

Fig. 1. Locations of the cormorant night roosts (*1–5*) and the colony (*6*) sampled in the Dutch Wadden Sea. *1* = De Schorren; *2* = Balgzand; *3* = Den Oever; *4* = Griend; *5* = Boschplaat; *6* = De Hond.

pellets were pooled. For analysis the pellets were defrosted and the mucous was dissolved in 1 M NaOH. It was checked that NaOH did not dissolve otoliths. Otoliths and other identifiable remains (e.g. pharyngeal bones, scales and claws of crustaceans) were collected and air-dried.

2.2. Estimating fish numbers and fish size

Otoliths were identified according to Härkönen (1986) in combination with our own reference collection. Each otolith was measured with a projection microscope (40×) if smaller than 4 mm in length or with vernier callipers if larger. Total length and width of each otolith were determined, except for broken ones, where usually only width could be measured. Other remains were not measured, but used for identification. Each otolith was identified as left, right or unknown and subsequently paired, on the basis of species, orientation, size, shape, wear and discoloration. Pairing was done conservatively, i.e. as many pairs of otoliths as reasonably possible were assigned from each individual sample. Pairs, as well as remaining single left and right otoliths, were each counted as one fish (Marteijn and Dirksen, 1991). For each sampling location, the mean number of fish per pellet was estimated. Fish size was reconstructed by taking the average size, as estimated from otolith length and width of all otoliths assigned to the same fish. Otoliths that were so badly worn (see below) that they could not reliably be measured were only counted, and for them, fish size was taken as the mean size for the 0-group for that species, based on other otoliths found.

All otoliths showed signs of wear, varying from only slight wear (class 1), to moderate (class 2), heavy (class 3) or extensive wear (class 4). The amount of wear was judged as follows: otoliths that were apparently complete, and still had irregular perimeters and a clearly visible sulcus (see Härkönen, 1986) were classed as 1; otoliths that were smooth, but still had some of the original perimeter structure and sulcus visible were classed as 2; those that had lost most of these features were classed as 3; otoliths that were even further reduced and in which size seemed to have no relationship any more to the original size were classed as 4. Length and width were measured in each otolith, and mean size for each species and wear class were calculated. Assuming that all otoliths had stemmed from the same populations of fish species, regardless of wear, sizes of class 2 and 3 otoliths were corrected to the size of class 1 otoliths. Since classification may have been biased, in that small otoliths may have had a relatively high probability of being classed as 2 or 3 rather than 1, we compared the resulting fish lengths with field data of length distribution. These data stemmed from a combination of a long-term series of fyke-net catches (see Philippart et al., 1996) and unpublished NIOZ data from catches of young fish on the tidal flats and in the tidal channels in the western Wadden Sea. From these sources, sufficient numbers were available for the main flatfish and gobies *Pomatoschistus* spp. A comparison of length–frequency distributions showed that we had overestimated original otolith sizes (Fig. 2). Hence, fish length was corrected downwards, by 28% in dab, 23% in plaice, 12% in flounder, 9% in sole and 10% in gobies. For other species we lacked data, but not correcting resulted in unrealistically high fish masses ingested. Therefore, we corrected in a similar way species with relatively smooth, thick, sturdy otoliths, such as sandeels or gadoids by 10% and other, thinner otoliths or otoliths with irregular perimeters or fragile tips, such as cyprinids, perches, smelt *Osmerus eperlanus* or clupeids, by 25%. The resulting fish lengths were then converted into fish mass by means of length–weight relationships from our reference collection for fish of the area. The sum of prey mass per pellet was considered to be an estimate

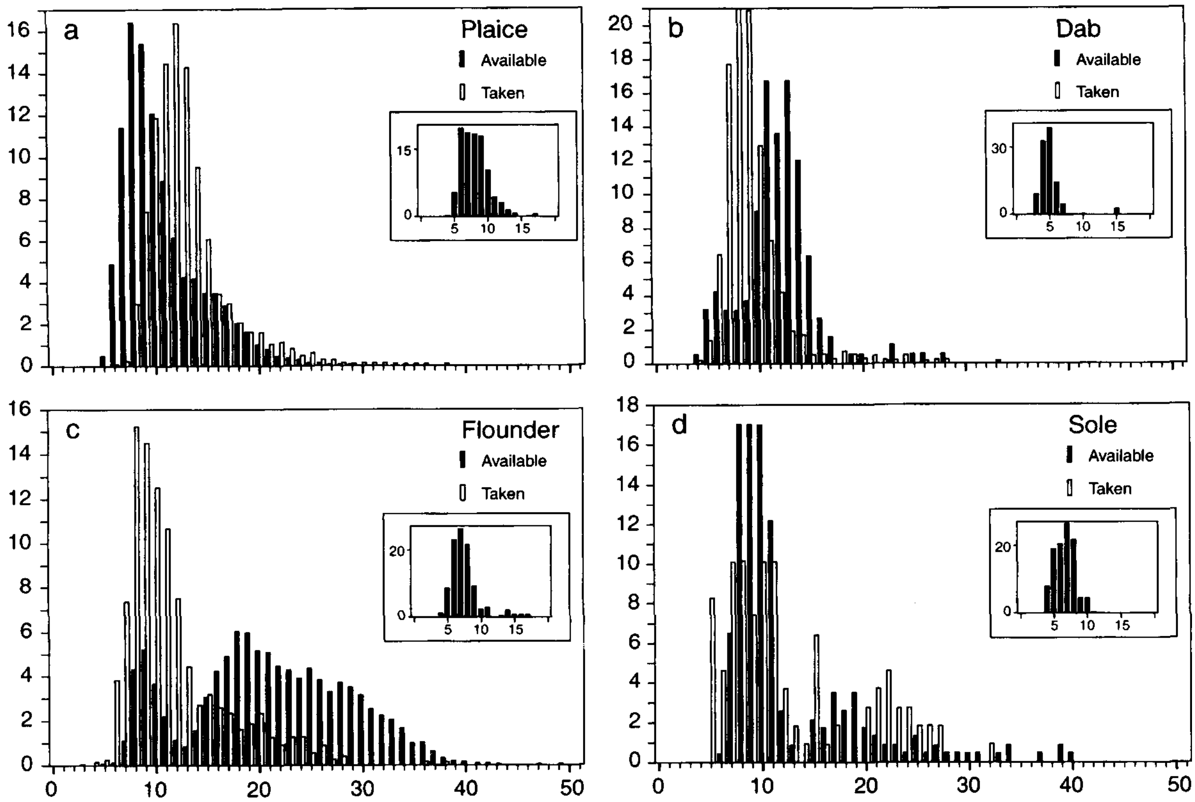

Fig. 2. Size (total length, cm) frequency distributions of juvenile flatfish in autumn in the Dutch Wadden Sea (black bars) and of consumed flatfish by cormorants, based on the sizes of the otoliths found in all pellets after correction for wear of class 2 and 3 otoliths to the size of class 1 otoliths (white bars). Flatfish availability was assessed from a long-term series of fyke-net catches (main figure) and from unpublished NIOZ data from catches of young fish on the tidal flats and in the tidal channels in the western Wadden Sea (inset).

of daily consumption. Recovery efficiency was estimated by comparing these estimated meal sizes with published information on daily food requirements.

2.3. Impact on juvenile flatfish stocks

Flatfish predation was estimated for each sampling location based on (1) the estimated number of bird days, (2) the mean number of flatfish present in the pellets, and (3) the assumption that each pellet contained remains of the fish eaten during the previous 24 hours (Duffy and Laurenson, 1983; Johnstone et al., 1990; Zijlstra and Van Eerden, 1995).

0-group flatfish absolute abundance in the Wadden Sea was estimated from a survey carried out in September 1987 as described in Bergman et al. (1989). The numbers of flatfish caught were corrected for distance trawled and net efficiency. For each tidal basin the mean density for the tidal flats and the subtidal was estimated and the total abundance was calculated. These 1987 flatfish data were converted into an abundance estimate for 1992 and 1993 by means of the data of the autumn survey (September) of the Demersal Young Fish Survey (DYFS) carried out annually since 1969 (see Van Beek et al., 1989).

3. Results

3.1. Cormorant abundance

Cormorant counts were available for 12 locations in 1992/1993, covering the main part of the popu-

Table 1
Mean monthly number of cormorants present at the various Wadden Sea islands and along the mainland of the Dutch Wadden Sea and number of bird days in 1992. Estimates are based on own observations and on data obtained from the SOVON database

Location	May	June	July	August	September	October
Wadden Sea islands						
Texel	400	400	500	600	800	300
Vlieland	50	0	100	100	200	70
Terschelling	100	1000	1000	1000	500	200
Ameland	20	50	30	50	30	10
Schiermonnikoog	20	20	40	60	50	10
Engelsmanplaat	20	40	80	70	70	20
Rottum	30	150	100	50	10	0
Griend	250	1000	1700	2000	1500	500
De Hond	150	200	400	400	300	100
Mainland						
Balgzand/Mokbaai	250	100	300	300	350	100
Wieringen	230	50	200	400	500	100
Northern coastline	100	200	150	100	150	50
Total	1620	3210	4600	5130	4460	1460
Days	31	30	31	31	30	31
Bird days	50220	96300	142600	159030	133800	45260

lation (Table 1). In general, the temporal pattern in abundance between the various locations was quite similar. At all locations, cormorant numbers started to build up in May, increased until August when in total over 5000 cormorants were present in the Dutch Wadden Sea and then numbers decreased again to a total of about 1400 birds in October. From November onwards only small numbers were found in the area.

3.2. Pellet analysis

In total 192 pellets were collected and examined, of which al least eight pellets did not contain identifiable fish remains (Table 2). On the basis of the number of empty pellets at other locations (8 out of 157), we assumed that 2 pellets within the pooled sample of 35 pellets from Boschplaat were empty, resulting in a total sample of pellets with fish remains of 182. In these, over 16,000 otoliths of at least 24 different fish species were found. A number of otoliths could not be identified to species level, only to family, viz. flatfish, goby, cyprinid or *Trisopterus* spp otoliths. Otoliths were found of five freshwater species, including one species (smelt) that occurs both in freshwater and in the marine environment, and of at least 19 marine species. Freshwater fish was found in the pellets from Balgzand (13%), Den Oever (56%) and De Hond (36%), locations in close proximity to freshwater habitats. Of the species found, only few were common. Flatfish were by far the most abundant group at each sampling location. Of other fish, only Gobiidae (15.3%) and Osmeridae (2.7%) accounted for more than 1% in numbers. Expressed in mass, flatfishes constituted 79% of the diet, percids 7% and cyprinids 5%. Bull-rout *Myoxocephalus scorpius*, smelt, twaite shad *Alosa fallax* and mackerel *Scomber scombrus* all contributed a little over 1% each. Other species, including crabs and shrimp were insignificant in this respect.

Flatfish dominated the diet and amounted to 73.2% of total numbers of fish found (Table 3). Proportions of flatfish ranged from 41% at Den Oever and 44% at De Hond to circa 80% at the other locations. Among the total of 3795 flatfishes identified to species, plaice was found most frequently (44.0%), followed by dab (30.2%), flounder (22.8%), sole (2.9%) and brill *Scophthalmus rhombus* (0.03%). Of a total of 157 individual pellets, 8 (5%) contained no prey remains and 21 (13%) contained only remains of freshwater fish (including smelt). Marine fish were found in 122 pellets (78%), and of these only 6 (5%) contained no flatfish otoliths. The mean number of flatfish found per pellet (only pellets with fish re-

Table 2
Species composition and absolute numbers of freshwater (F) and saltwater (S) fish and crustaceans eaten by cormorants in the Dutch Wadden Sea based on otolith recovered from pellets collected at the various roosts in August 1993 and at the colony De Hond in September 1992

Order	Family	Latin name	Species name	F/S	De Schorren	Balgzand	Den Oever	Griend	Boschplaat	De Hond	Total
Pleuronectiformes	Pleuronectidae	*Pleuronectes platessa*	plaice	S	309	247	96	709	237	57	1655
		Limanda limanda	dab	S	216	86	38	527	179	100	1146
		Platichthys flesus	flounder	S	266	57	118	130	238	46	855
	Bothidae	*Scophthalmus rhombus*	brill	S					1		1
	Soleidae	*Solea solea*	sole	S	38	9	2	10	41	8	108
			unidentified	S	522	289	186	1292	554	55	2898
Perciformes	Percidae	*Gymnocephalus cernuus*	ruffe	F			7			23	30
		Perca fluviatilis	perch	F		65	412			19	496
	Carangidae	*Trachurus trachurus*	scad	S	1						1
	Zoarcidae	*Zoarces viviparus*	eelpout	S	1		2				3
	Pholididae	*Pholis gunnellus*	butterfish	S			12			10	22
	Ammoditydae		sandeel sp.	S	2	1		23	6	7	39
	Callionymidae	*Callionymus lyra*	dragonet	S					38		38
	Gobiidae		goby sp.	S	376	48	11	545	271	96	1347
	Scombridae	*Scomber scombrus*	mackerel	S		6					6
Salmoniformes	Osmeridae	*Osmerus eperlanus*	smelt	F/S			149	3		89	241
Scorpaeniformes	Triglidae		gurnard sp.	S		1			5		6
	Cottidae	*Myoxocephalus scorpius*	bull-rout	S	7	3	4		1	7	22
	Cyclopteridae	*Cyclopterus lumpus*	lumpsucker	S				1			1
Gadiformes	Gadidae	*Trisopterus* luscus	bib	S		2					2
		Trisopterus sp.	bib / poor cod		1		2				3
		Merlangius merlangus	whiting	S	3		1	1	2	1	8
		Pollachius pollachius	pollack	S		1					1
Clupeiformes	Clupeidae	*Alosa fallax*	twaite shad	S		7					7
Cypriniformes	Cyprinidae	*Rutilus rutilus*	roach	F		12	7				19
		Rutilus erythrophthalmus	rudd	F		19					19
			unidentified	F		18	20			88	126
Crustacea, Decapoda	Portunidae	*Carcinus maenas*	shore crab	S	1			2			3
	Crangonidae	*Crangon crangon*	common shrimp	S	174	201	55	357	28	162	977
Total number of fish					1742	871	1067	3241	1573	606	9100
Number of fish species					≥11	≥15	≥14	≥9	≥11	≥13	≥24
Number of pellets					30	30	25	38	35	34	192
Empty pellets					1	2	0	1	(2)	4	10

Table 3
Percentages (% of numbers) of freshwater and marine prey (including flatfish) and flatfish separately, per sampling location. Data from Table 2

Species	De Schorren	Balgzand	Den Oever	Griend	Boschplaat	De Hond	Total
Freshwater fish	0	13	56	0.1	0	36	10.2
Marine fish	100	87	44	99.9	100	64	89.8
Flatfish	78	79	41	82	79	44	73.2

Table 4
Mean number of flatfish found per cormorant pellet with fish at the various locations in the Dutch Wadden Sea. Data from Table 2; Unidentified flatfish (i.e. plaice/dab/flounder) have been assigned to the various species according to their relative abundances per sample

Latin name	Species name	De Schorren	Balgzand	Den Oever	Griend	Boschplaat	De Hond	Total
Pleuronectes platessa	plaice	17.69	15.36	6.68	37.13	13.27	2.4	16.45
Limanda limanda	dab	12.38	5.36	2.64	27.41	10.03	4.23	11.25
Platichthys flesus	flounder	15.24	3.54	8.20	7.03	13.33	1.93	8.26
Scophthalmus rhombus	brill					0.03		0.01
Solea solea	sole	1.31	0.32	0.08	0.27	1.24	0.27	0.59
Total per pellet		46.62	24.57	17.60	72.10	37.91	8.83	36.56
Pellets with fish		29	28	25	37	33	30	182

mains included) was 36.6, but differed between locations (Table 4). The highest mean number of flatfish was observed at Griend, 72 flatfish per pellet, while at De Hond only 9 flatfish per pellet were found. On average, plaice was most abundant (about 16 fish per pellet), followed by dab (11 fish per pellet) and flounder (about 8 individuals per pellet). Sole was only rarely taken, with on average 0.6 fish per pellet with fish. Predation on flatfish differed per location and was highest at the most seaward roosts (Griend, De Schorren, Boschplaat), while cormorants roosting near large freshwater bodies (De Hond, Den Oever, Balgzand) had also ingested significant quantities of freshwater fish (Table 2).

The sizes of the flatfish consumed were reconstructed from otolith–fish size relationships (Table 5) after correction for wear. Almost all flatfish were juveniles, mainly 0-group, i.e. fish smaller than 14 cm total length (Fig. 2). Flatfish over 20 cm total length were rarely taken. Only sole showed some selection for larger individuals, but in this species too, mainly 0-group fish were taken. Considering only 0-group flatfish, and distributing the unidentified (non-sole) flatfish over plaice, dab and flounder, according to their respective numbers of identified fish at each location, total numbers of 0-group flatfish found in 182 pellets amounted to 6318, comprising 44.9% plaice, 32.9% dab, 21.0% flounder and 1.2% sole.

The estimated daily consumption differed considerably both between pellets and, to a lesser extent, also between locations (Figs. 3 and 4). On average, consumption amounted to about 460 g of fish and 2 g of crustaceans, pellets without food remains excluded. Published information on daily food requirements, based on experiments in captivity, reported a daily consumption of at least about 500 g wet weight (Zijlstra and Van Eerden, 1995), suggesting an average recovery efficiency of about 90%. Cormorant food requirements may also be estimated allometrically. An average cormorant of 2200 g has a predicted Basal Metabolic Rate of 889 kJ d^{-1}, which translates into a Field Metabolic Rate of 2222 kJ d^{-1}. Assuming food utilisation efficiencies of 80% for fish-prey and 70% for crustaceans, and energetic contents of 6.5 kJ kg^{-1} for marine fish species with high fat contents (Clupeidae, Ammodytidae, Scombridae, Osmeridae), 4 kJ kg^{-1} for other marine fish and crustaceans (see Tasker and Furness, 1996) and 5 kJ kg^{-1} for Percidae and Cyprinidae, the mean intake, as inferred from the contents of pellets with

Table 5
Relationships between total fish length (FL, cm) and otolith length (OL, mm) and otolith width (OW, mm) and between total fish length and fish mass (Mass, g wet weigth) for the various fish species, together with regression coefficient (R^2) and number of observations (n)

Species name	FL = a(OL)^b				FL = c(OW)^d				Mass = e(FL)^f			
	a	b	R^2	n	c	d	R^2	n	e	f	R^2	n
Plaice	3.5352	1.1255	0.99	744	4.6440	1.2704	0.99	779	0.0099	3.0209	0.99	345
Dab	3.0857	1.2664	0.98	498	4.4721	1.4077	0.98	503	0.0067	3.1389	0.99	225
Flounder	3.3615	1.2217	0.97	543	4.9929	1.3681	0.96	581	0.0103	2.9976	0.99	316
Brill	4.5332	1.1496	0.96	91	6.7414	1.1381	0.97	111	0.0114	3.0846	0.99	58
Sole	5.5255	1.2364	0.97	634	5.9738	1.3430	0.97	639	0.0072	3.0646	0.99	225
Scad	3.0568	0.9937	0.99	505	5.2168	1.1677	0.98	580	0.0098	2.9806	0.99	203
Eelpout	7.4171	1.1386	0.89	249	13.4200	1.3904	0.92	279	0.0023	3.3101	0.99	152
Butterfish	9.9258	0.8658	0.91	93	18.7100	0.9362	0.84	99	0.0011	3.4752	0.97	66
Goby sp.	3.3860	1.1262	0.95	636	3.4793	1.3655	0.96	635	0.0113	2.8799	0.98	331
Sandeel sp.	6.0770	0.9079	0.94	487	11.0430	1.0200	0.92	497	0.0010	3.4040	0.98	210
Dragonet	3.7156	1.5300	0.96	433	11.5580	1.4998	0.96	481	0.0078	2.9613	0.99	257
Mackerel	7.2790	1.0780	0.86	67	19.8900	1.2347	0.83	150	0.0138	2.8249	0.97	66
Smelt	2.9761	1.1165	0.98	276	4.1693	1.3263	0.97	382	0.0023	3.3764	0.99	191
Gurnard sp.	4.3903	1.3718	0.96	689	5.9114	1.4283	0.96	692	0.0088	2.9978	0.99	373
Bull-rout	2.9738	1.0363	0.94	337	5.7867	1.1327	0.94	356	0.0092	3.1850	0.99	170
Lumpsucker	9.1271	2.1572	0.92	93	19.9520	2.1729	0.93	93	0.0338	3.1015	0.99	72
Trisopterus sp.	1.0145	1.3760	0.96	541	3.0758	1.3335	0.93	601	0.0062	3.2055	0.99	184
Whiting	2.0564	0.9446	0.99	542	4.8369	1.1378	0.98	619	0.0061	3.0845	0.99	300
Pollack	1.3238	1.3430	0.98	129	4.2831	1.3688	0.96	136	0.0042	3.2691	0.97	63
Twaite shad	5.2347	1.5246	0.98	286	12.0620	1.6628	0.98	302	0.0059	3.0777	0.99	185
Roach/rudd	7.7817	0.8176	0.94	31	7.6325	0.7893	0.47	31	0.0040	3.3990	0.99	16

Note: for percidae the equations from Veldkamp (1994) were used.

fish, may be estimated as 1570 kJ d^{-1}, assuming that each pellet with prey represents the prey eaten during one day. This amount suggests a lower recovery efficiency of about 70%.

3.3. Flatfish abundance

The mean densities and absolute abundances of flatfish in 1987 for each tidal basin are presented in Table 6. In total 213 million juvenile flatfish were present. The most abundant species were plaice (87.6 million) and sole (82.5 million), followed by dab (34.8 million) and flounder (8.1 million). Local abundance differed with respect to tidal basin, tidal/subtidal habitat and species. In plaice and flounder, the contribution of the tidal flat areas was most important, while for sole and dab most individuals were caught in the subtidal. The relative abundance of the various 0-group flatfish species (all fish <14 cm) in the autumn DYFS survey over the years are presented in Fig. 5. The absolute abundance estimated for 1987 corresponded with the relative indices of the DYFS in 1987: plaice and sole were the most abundant species, followed by dab and flounder. With the DYFS indices of 1987 and 1992/1993, the abundance estimates for 1987 were converted into abundance estimates for 1992 and 1993. For dab and flounder they were in the same order of magnitude, for plaice and sole the figures were much lower.

The size-frequency distributions varied between the species (Fig. 2). The smallest sizes were found in dab, with peak numbers at a size of 5 cm total length. In sole and flounder, the peak numbers had a size of about 7 cm, while in plaice the peak was about 8 cm. The fyke catches showed slightly larger average sizes, suggesting that this device did not catch the smallest sizes as well as the larger individuals of the 0-group flatfishes.

3.4. Predation pressure

The total predation pressure by cormorants on 0-group flatfish was estimated under the assumption

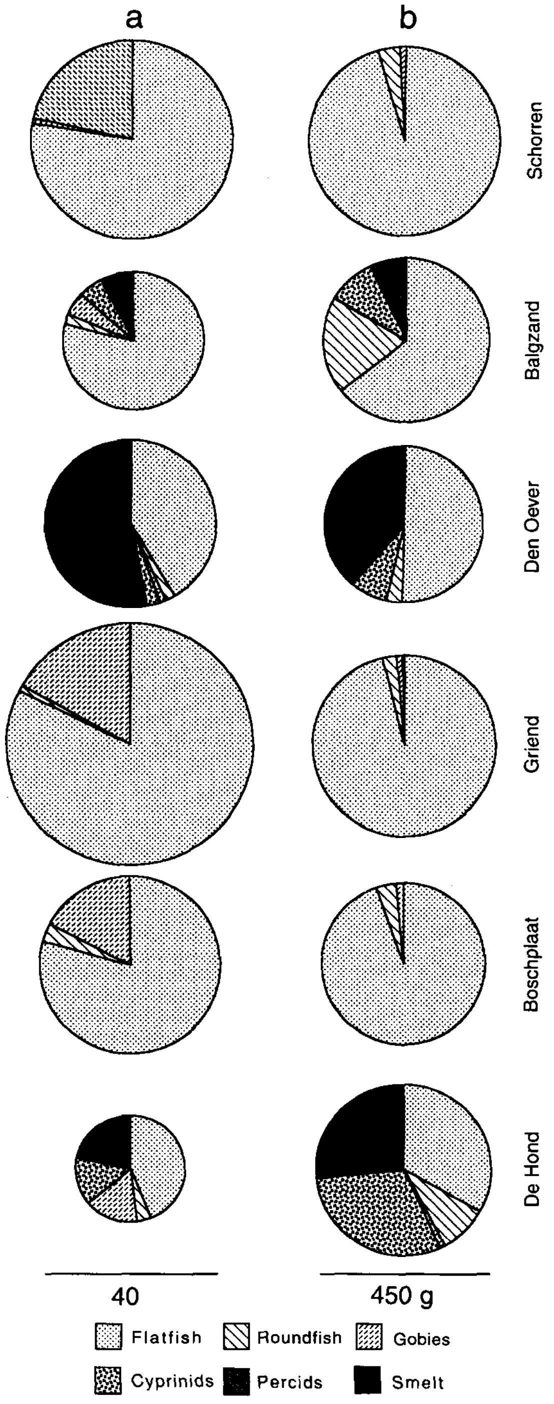

Fig. 3. Mean contribution in numbers (a) and in mass (b) of various prey groups found in the cormorant pellets at the various sampling stations, reconstructed from otoliths found in the pellets. Circle diameters indicate average numbers of ingested fish, respectively average mass, per pellet, per location.

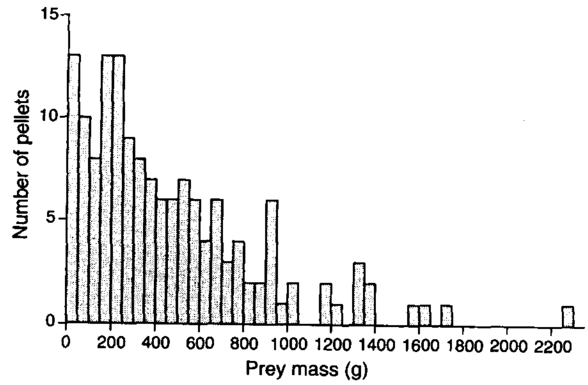

Fig. 4. Frequency distribution of estimated daily consumption of cormorants based on the sum of reconstructed prey mass per pellet by means of otolith–prey length and prey length–prey mass relationships from the NIOZ-IBN reference collection.

that each pellet with fish contained the remains of the fish eaten during 24 hours and that the diet was similar in 1992 and 1993 and from May to October. For each area, the number of bird days was estimated for each month (Table 1) and multiplied by the mean number of flatfish present in the pellets (Table 4). For locations with cormorants where no pellets were collected, diet composition was assumed to be similar to that of nearby, similar locations: for the Wadden Sea islands of Vlieland, Ameland, Schiermonnikoog, Engelsmanplaat and Rottum average values between diet compositions at the islands of Texel (De Schorren) en Terschelling (Boschplaat) were used, while the diet of cormorants roosting along the northern mainland shores was assumed to be intermediate

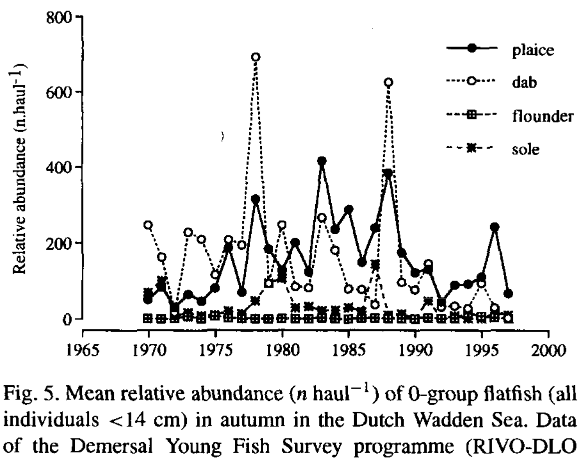

Fig. 5. Mean relative abundance (n haul^{-1}) of 0-group flatfish (all individuals <14 cm) in autumn in the Dutch Wadden Sea. Data of the Demersal Young Fish Survey programme (RIVO-DLO unpubl.).

Table 6
Mean density (n 1000 m^{-2}) and absolute numbers of juvenile flatfish in the various tidal basins of the Dutch Wadden Sea at the tidal flats (T), in the subtidal (S) and combined (T + S)

Tidal basin	Mean density (n 1000 m^{-2}) T	S	T + S	Total abundance ($\times 10^{-6}$) T	S	T + S
Plaice						
Marsdiep	38.1	12.1	18.1	4.8	5.1	9.9
Eierlandse Gat	60.5	22.0	51.4	7.0	0.8	7.8
Vlie	38.4	50.7	43.9	12.5	13.4	25.9
Borndiep	39.5	32.1	37.7	8.0	2.0	10.0
Pinkegat	78.8	18.5	70.2	4.5	0.3	4.8
Friesche Zeegat	47.9	37.2	45.5	4.6	1.0	5.6
Eierlanderbalg	112.0	5.1	95.0	3.6	0.1	3.7
Lauwers Schild	96.3	12.4	80.7	10.6	0.3	10.9
Ems–Dollard	30.7	13.5	25.2	7.5	1.5	9.0
Total				63.1	24.5	87.6
Dab						
Marsdiep	0.0	0.5	0.4	0.0	0.2	0.2
Eierlandse Gat	0.0	7.2	1.7	0.0	0.3	0.2
Vlie	0.0	91.2	40.9	0.0	24.0	24.0
Borndiep	0.7	12.8	3.6	0.2	0.8	1.0
Pinkegat	0.0	0.0	0.0	0.0	0.0	0.0
Friesche Zeegat	0.4	39.0	8.9	0.1	1.0	1.1
Eierlanderbalg	0.0	10.5	1.6	0.0	0.2	0.2
Lauwers Schild	3.3	1.75	3.0	0.4	0.1	0.5
Ems–Dollard	1.9	0.8	1.5	7.5	0.1	7.6
Total				8.0	26.8	34.8
Sole						
Marsdiep	1.2	0.0	0.3	0.2	0.0	0.2
Eierlandse Gat	0.0	41.3	9.8	0.0	1.5	1.5
Vlie	1.1	2.5	1.7	0.3	0.7	1.0
Borndiep	17.5	27.8	20.0	3.5	1.7	5.3
Pinkegat	3.0	32.8	7.8	0.2	0.5	0.7
Friesche Zeegat	10.9	487.4	115.5	1.0	13.1	14.2
Eierlanderbalg	1.0	7.7	2.0	0.0	0.2	0.2
Lauwers Schild	7.0	56.7	16.2	0.8	1.4	2.1
Ems–Dollard	95.3	307.1	162.9	23.3	34.1	57.4
Total				29.3	53.2	82.5
Flounder						
Marsdiep	0.6	0.0	0.1	0.1	0.0	0.1
Eierlandse Gat	2.0	0.0	1.5	0.2	0.0	0.2
Vlie	8.7	3.9	6.5	2.8	1.0	3.8
Borndiep	0.0	0.0	0.0	0.0	0.0	0.0
Pinkegat	0.7	0.0	0.6	0.0	0.0	0.0
Friesche Zeegat	1.2	0.8	1.1	0.1	0.0	0.1
Eierlanderbalg	0.0	2.7	0.4	0.0	0.1	0.1
Lauwers Schild	0.9	0.0	0.7	0.1	0.0	0.1
Ems–Dollard	10.7	8.6	10.1	2.6	1.0	3.6
Total				6.0	2.1	8.1

Table 7
Total stage mortality (Mt, -) and instantaneous daily mortality rate (M, d^{-1}) of predation by cormorants from July through September (92 days with peak numbers of birds in the area) on 0-group flatfish in the Dutch Wadden Sea. Abundance data according to autumn flatfish surveys in September; predation not corrected for recovery efficiency

	Abundance September ($\times 10^{-6}$)	Predation Jul–Sep ($\times 10^{-6}$)	Mt (-)	M (d^{-1})
1992				
Plaice	16.4	8.97	0.436	0.0047
Dab	28.9	6.76	0.210	0.0023
Sole	0.8	0.19	0.213	0.0023
Flounder	2.3	3.53	0.930	0.0101
1993				
Plaice	33.0	8.97	0.240	0.0026
Dab	31.8	6.76	0.193	0.0021
Sole	4.4	0.19	0.042	0.0005
Flounder	5.9	3.53	0.469	0.0051

between those at Balgzand and Den Oever, both also along the mainland coast.

In total about 27.5 million 0-group flatfish were consumed (Table 7). 0-group plaice (12.55 million) were most often taken, followed by dab (9.45 million), flounder (5.17 million) and sole (0.29). Consumption of flatfish was lowest at De Hond in the eastern part of the Dutch Wadden Sea and at Den Oever in the western part. Most 0-group flatfish were consumed at Griend (some 15 million), followed by De Schorren and Boschplaat (some 4 million each).

An estimate of the mortality induced by cormorant predation was calculated for the period when peak numbers were present in the Wadden Sea (July through September) by comparing the amount of flatfish consumed by cormorants with the abundance estimates of the various flatfish for 1992 and 1993 (Table 7), according to:

$$N_t = N_0 \cdot e^{-Mt}$$

in which N_t is the abundance of the flatfish in September; N_0 is the sum of the abundance of the flatfish in September and of the estimated amount predated by the cormorants; t is time of predation in days (92) and M is the daily instantaneous mortality rate (d^{-1}). Total stage mortality (Mt) over these three summer months varied between 0.930 for flounder and 0.210 for dab in 1992 and between 0.469 for flounder and 0.042 for sole in 1993 (Table 7). M differed in a similar way in 1992 between 0.0101 d^{-1} for flounder and 0.0023 d^{-1} for dab, and in 1993 between 0.0051 d^{-1} for flounder and 0.0005 d^{-1} for sole.

4. Discussion

4.1. Sampling strategy

The sampling design of both the analysis of the predation by cormorants and of the flatfish survey might have introduced some bias. Pellets have only been collected in August and September. Although cormorants are most abundant in the area during these months and the intake in this period will greatly influence total intake over summer, any seasonal variation in the diet of the cormorants, e.g. in response to changes in the prey fish community (Pilon et al., 1983; Rail and Chapdelaine, 1998), is not taken into account in the estimation of the number of flatfishes consumed and the estimate of total numbers taken may thus be slightly biased.

The reconstruction of the pellet content of cormorants is based on the recovery of the otoliths in the pellets. Experimental data indicate that recovery rates of otoliths may be considerably less than 100%. Duffy and Laurenson (1983) found recovery rates of only 33%; Zijlstra and Van Eerden (1995) found 52% of the otoliths ingested by cormorants in the pellets. Johnstone et al. (1990) found species-specific recovery rates of 72% for large cod *Gadus morhua* otoliths and of 22% for small sprat *Sprattus*

sprattus otoliths. Empty pellets were also rather frequently observed, 20% by Zijlstra and Van Eerden (1995), while in this study at least 8 pellets and another estimated 2 for the pooled Boschplaat sample, or 5.2%, contained no fish remains. Furthermore, the frequency distribution of estimated daily intakes shows a considerable number of pellets with less than 250 g, i.e. less than half the estimated required intake. On the other hand, total ingested masses of over 1000 g were found in 12 pellets, and these seem unrealistically high. Very low estimated intakes may be due to poor recovery of otoliths, to total loss of otoliths of certain species of fish or to the fact that in late summer, a large proportion of the birds are juvenile, and therefore likely to be sub-optimal foragers. It is a fact that not all otoliths were recovered, as not all could be paired. This was partly compensated for by considering single otoliths as single fish, but if both otoliths of a pair are missing, the number of fish is underestimated. Also, some common species of fish with otoliths known to be fragile or very small, e.g. herring *Clupea harengus*, sprat *Sprattus sprattus* and pipefish *Syngnathus* sp., were not found at all, even though these fish might sometimes be important prey (Leopold and Winter, 1997; Leopold, unpubl.). Very high estimated intakes may be the result of birds retaining in the stomach otoliths from a longer period than just one day. This could result in both the production of empty pellets (pellet produced, but otoliths not included) and in the production of pellets with prey remains from two days (produced the next day); the latter can also be caused by a pellet production rate of less than once a day, e.g. in young birds (Trauttmansdorff and Wassermann, 1995). Part of the difference between estimated intake and estimated required intake can thus be explained by loss of otoliths, and by comparing estimated intake with estimated food requirements we estimated that recovery rate was somewhere between 70 and 90%. However, cormorants in the Netherlands generally have a relatively low intake of fish in late summer (Van Dam et al., 1995) when large numbers of inexperienced foragers enter the population, and if this resulted in a lower average daily consumption, the magnitude of otolith loss will have been less. Estimated mean fish meal size (about 460 g wet weight) is only marginally lower than estimated daily food requirements, considering the influx of young birds into the population at the time of estimation of intake. Still, the estimated number of flatfish in the pellets should be considered a slight underestimation, due to otolith loss, even if the difference is made up largely by missing otoliths from other species. Moreover, if empty pellets had been included in the calculation of average ingested prey mass, because such empty pellets are thought to correspond to an equal number of pellets containing the remains of two days of foraging, then the grand total of 192 pellets should have been used in calculating average intake. Average intake would then have been 436 gram or 65% of the amount needed in theory.

Secondary consumption of fish might be another source of bias resulting in an overestimation of the number of fish eaten and hence also in an underestimation of otolith loss. Blackwell and Sinclair (1995) found clear evidence of secondary consumption of fish by double-crested cormorants in Maine, USA. However, with flatfish predation by cormorants in the Dutch Wadden Sea this is less likely. Firstly, cannibalism of flatfish as observed in British waters (Macer, 1967; Edwards and Steele, 1968) has not been found in the Dutch Wadden Sea (Kuipers, 1977; De Vlas, 1979), and secondly otoliths of potential predators of juvenile flatfish were rare in the cormorant pellets in this study. The crabs and shrimp might have been secondary prey, but these contributed little to the birds' intake.

The size of the prey consumed was based on the length and the width of the otoliths found in the pellets, after a correction for wear. Comparing the resulting length–frequency distributions of the most relevant species in the pellets with those in the field indicated that we had over-corrected for wear, by assigning too many small otoliths to the highest wear-class. This over-correction was re-corrected before fish mass was calculated, but this procedure is rather cumbersome and sensitive to errors. As length–mass relationships are power curves, a small error in estimated fish lengths results in a much larger error in estimated prey mass. Therefore, all estimates of intake from otoliths should be taken with caution and not as evidence of for instance substantial loss of otoliths. We therefore consider the prey spectrum and the relative contribution of the various species to the diet fairly accurate, with the possible exception of clupeids and other fish with very small or fragile otoliths.

The main result, that small flatfish should be considered the main prey of great cormorants in the Wadden Sea, is corroborated by a recent study in the German part of the Wadden Sea (Nehls and Gienapp, 1997).

The estimate of the absolute abundance of juvenile flatfish in the Wadden Sea was based on a survey carried out in autumn 1987 by means of a beam-trawl, a fishing gear optimal for flatfish sampling. However, the survey was restricted to areas where sampling was possible, omitting for instance extremely silty stations. Since juvenile flounder has a preference for muddy areas (Van der Veer et al., 1991), their numbers might have been underestimated.

4.2. Predation on flatfish

In total more than 20 different fish species were found in the pellets, including four freshwater species: roach *Rutilus rutilus*, rudd *R. erythrophthalmus*, perch *Perca fluviatilis*, ruffe *Gymnocephalus cernuus* and one brackish water species: smelt. Studies in colonies near freshwater bodies in the Netherlands showed these fish species to be important prey items (Voslamber, 1988; Dirksen et al., 1990; Marteijn and Dirksen, 1991; Veldkamp, 1994; Van Dam et al., 1995). Cormorants are considered to be opportunistic feeders, which means that the diet composition is determined by the relative availability of the various fish species (Pilon et al., 1983; Martucci and Consiglio, 1991; Suter, 1997). The data in this study do not show a clear species preference, but indicate that cormorants take whatever fish species is readily available. Most of the saltwater fish caught by the cormorants are demersal species, but most of the freshwater fish are pelagic. In the Dutch Wadden Sea, 65% of all the fish can be considered demersal, the majority being flatfish (Hovenkamp and Van der Veer, 1993).

Flatfish comprise the most important group in the diet of great cormorants in the Wadden Sea (this study; Nehls and Gienapp, 1997). Also Steven (1933), Mills (1969) and Richner (1995) found the food of cormorants to be mainly flatfish: 40 to 85% of the diet. In the Dutch Wadden Sea similar percentages have been found, 41 to 83% between sites. Even at De Hond and Den Oever where freshwater fishes were locally abundant, flatfish still outnumbered all other fish species in the pellets. Most fish were small (0-group) and the birds apparently avoided large flatfishes. Flatfish width, rather than length sets a limit for ingestion by a gape-limited predator such as the cormorant (Winter and Leopold, 1993), as also indicated by the fact that sole, a less wide flatfish, was taken to greater lengths.

In total cormorants appeared to catch roughly 28.6 million flatfish in the Dutch part of the Wadden Sea during summer, of which 27.5 million were 0-group fish. Some bias may have been introduced here, as all class 4 otoliths (extensive wear) were considered to belong to 0-group fish. This was probably true for the vast majority of these otoliths, but some otoliths of larger fish might also have been reduced to a very small size and hence been miss-classified in this respect (Suter and Morel, 1996); this would result in a slight overestimation of the predation pressure on the 0-group. Although cormorants are present year round, 70% of the number of bird days — and hence of the predation — occurs from July to September. Information about the total mortality of juvenile flatfish in the Wadden Sea is restricted to plaice. Beverton and Iles (1992) have calculated an average stage mortality of 0-group plaice of 0.88 between the beginning of July and the end of September, the period when cormorants are most numerous in the Wadden Sea (Table 1). During this period the stage mortality induced by cormorant predation accounted for 0.436 (49.5% of total stage mortality) and 0.240 (27.3%) in 1992 and 1993, respectively. The DYFS survey data show that the abundance of 0-group plaice and also of the other species was very low in 1992 and 1993. Up to 10 times more abundant year classes have been found in other years. Under these conditions the impact of cormorant predation will be much lower and even insignificant, even though the birds may take even higher proportions of flatfish as prey in years when these are more abundant. It is noteworthy that only at De Hond, where pellets were collected in 1992 when plaice were half as numerous in the Wadden Sea as in 1993 (Table 7), did dab outnumber plaice as prey (Table 2). For the other flatfish species, dab, sole and flounder, no quantitative estimates of the mortality during the 0-group is available. However, relative predation pressure in dab is probably similar to that in plaice, while sole were taken in lower numbers and flounder in higher numbers than would be expected on the basis of their abundance. This suggests that, by different behaviour or habitat choice, sole avoid detection by cormorants more successfully than do the other flatfish species in the Wadden Sea. Flounder on the other hand, seems relatively vulnerable to predation by cormorants, or was under-sampled in the flatfish surveys. Many assumptions were made to arrive at the estimation of total cormorant predation pressure on juvenile flatfish. All are subject to considerable uncertainty. None of the figures used for fish-stocks, area used for foraging for the birds, bird numbers, numbers and sizes of prey eaten and numbers of fish not represented by their otoliths in the pellets should be seen as figures that are necessarily quantitatively correct. Therefore, questions remain as to how large exactly is the total amount of fish taken by the birds over summer, in relation to numbers available. In conclusion, however, 0-group flatfish comprise a considerable amount of cormorant diet in the Dutch Wadden Sea. Secondly, cormorant predation appears to be an important source of mortality, particularly in years with a low 0-group stock size. This supports results from other studies on cormorants (Mills, 1969; Barrett et al., 1990; Van Dam et al., 1995), in that these birds can have a serious effect on fish stocks.

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