# Diets of shags *Phalacrocorax aristotelis* and cormorants *P. carbo* in Norway and possible implications for gadoid stock recruitment

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ABSTRACT: The diets of shags and cormorants were studied in Norway through analyses of regurgitated pellets. Although this method has many limitations, indications were that both species rely heavily on small gadoids (Gadidae) and sand eels (Ammodytidae) for food throughout their range, but also eat other fish species when available. There was considerable dietary overlap between species, despite a tendency for cormorants to eat larger fish and more benthic items than shags. Predation by shags and cormorants could be a factor limiting the recruitment of cod and saithe into what are now severely reduced, but commercially important stocks in the Norwegian and Barents Seas.

# INTRODUCTION

There is an increasing awareness of the roles of seabirds in marine ecosystems (e.g. Croxall et al. 1985, Schneider et al. 1986, Croxall 1987) and recent estimates in areas of major seabird concentrations are of substantial energy harvest by these top predators (e.g. Brown & Nettleship 1982, Furness 1982, Croxall 1987, Cairns et al. 1990). It has also been suggested that seabirds may deplete prey biomass around colonies (Gaston et al. 1983, Furness & Birkhead 1984, Hunt et al. 1986), direct evidence for which has been presented for double-crested cormorants *Phalacrocorax auritus* (Birt et al. 1987).

Shags *Phalacrocorax aristotelis* and cormorants *P. carbo* are large marine birds, ca 2 and 3 kg respectively, and their daily food consumption has been estimated as 16 to 30 % of body weight (Madsen & Spärck 1950, Dunn 1975, Johnstone et al. 1990). What and how much these species eat have long been of concern to fishermen, fisheries biologists and, most recently fish farmers (e.g. Steven 1933, Lumsden & Haddow 1946, Rae 1969, West et al. 1975, Barlow & Bock 1984, Craven & Lev 1987, Kennedy & Johnston 1987, Moerbeek et al. 1987). Concern has however often been based on anecdotal evidence and popular opinion, rather than on

scientific study. Although commercial species have repeatedly been found in the diets of shag and cormorants in e.g. Britain, Canada and Australia, their consumption is now usually judged to be inconsequential to fisheries (Lumsden & Haddow 1946, Rae 1969, West et al. 1975, Pilon et al. 1983, Barlow & Brock 1984, Trayler et al. 1989).

Saithe Pollachius virens and cod Gadus morhua are both commercially important species in the Norwegian and Barents Seas and are heavily exploited by several nations. In recent years their stocks have dropped considerably – cod by ca 80 % since the early 1950s, saithe by 50 % since 1970 (Anonymons 1989), causing much concern for fisheries managers. As a result, factors affecting gadid recruitment have become a recent focus of research attention (e.g. Loeng 1987), but as yet the potential predation pressure of seabirds has not been considered to be significant. This study investigates avian predation on these fish.

Shags and cormorants breed in colonies all along the Norwegian coast, and breeding populations have recently been estimated to be 15000 and 21000 pairs, respectively (Røv 1984, Røv & Strann 1986). The breeding ranges of shags and cormorants overlap from Trondheim northwards. Data concerning the diet of shags in Norway are limited to a few samples from Hornøy, East Finnmark (Furness & Barrett 1985, Barrett et al. 1986). Apart from anecdotal data collected by Collett (cited in Madsen & Spärck 1950) at the turn of the century, the diet of Norwegian cormorants is unknown. The present study further documents the diets of shags and cormorants across most of their Norwegian breeding range through data collected in 1985 to 1989 at 8 shag colonies, 5 cormorant colonies and one cormorant roosting site. The study also assesses the potential effects of these species on commercial fish stocks and expands studies by Lack (1945) and Ainley et al. (1981) of habitat partitioning (diet overlap) among Phalacrocoracidae in areas of sympatry. Comparisons are also made with other studies of shag and cormorant diet in Britain and North America.

# MATERIAL AND METHODS

Cormorants and shags regurgitate pellets of undigested material at least once per day (Ainley et al. 1981, Duffy & Laurenson 1983, Johnstone et al. 1990), and their contents give a useful indication of what the birds have recently eaten. As a food sampling method, the analysis of pellets has very clear limitations. Pellet contents do not necessarily reflect the complete diet of shags or cormorants, nor do the size of otoliths recovered seem to yield more than a rough approximation, and sometimes, because of digestion, an underestimation, of the size of fish eaten (Ross 1976, Duffy & Laurenson 1983, Jobling & Breiby 1986, Gales 1988, Johnstone et al. 1990). These pellets can, however, be sampled cheaply and with a minimum of disturbance. Unless detailed quantitative data are needed for the assessment of complete diet breadth or total food consumption, this method is simple, valuable and far preferable to forcing birds to regurgitate or even killing them (see Duffy & Jackson 1986 for a review of methods of food sampling). Even though otolith wear can vary from bird to bird or time to time (Johnstone et al. 1990), such pellet analysis is, in our and Duffy & Laurenson's (1983) opinion, a useful, non-destructive tool with which to study, if only roughly, temporal, spatial and interspecific variations in diet composition.

For this study, pellets regurgitated by incubating or brooding shags were collected over periods of several weeks from nest sites on Hornøy (June to July 1989) and Bleiksøy (July 1985, May to August 1986) in northern Norway (by R. T. B. and W. A. M.) and from 6 breeding colonies (Ferkingstadøyane, Urter, Låtersøy, Melne, Lyngsøy, and Spannholmane) in Rogaland in June and July 1988 (by J. L.) (Fig. 1). Cormorant pellets were collected during single day visits to breeding sites on 3 colonies in East Finnmark (2 in Sør-Varanger and 1 in Kongsfjord) in 1989 (by N. R.), on Hovsflesa, in



Fig. 1. Localities where shag (●) and cormorant (○, △) diets were studied in Norway. (Six neighbouring colonies in Rogaland have been pooled). (●, ○) Breeding sites; (△) roost

Lofoten. in July 1985 and July 1986 (R. T. B. and W. A. M.) and at Vikna, Trøndelag in July 1887, and to a roost on Munkholmen, Trondheimsfjord in September and October 1986 (N. R.). Except for those collected in East Finnmark, each pellet was bagged separately and stored either in a deep freezer or in alcohol before being sorted under a binocular microscope in the laboratory by the respective collectors. East Finnmark samples were collected and frozen in a single bag for each colony.

Fish were identified to lowest possible taxon by sagittal otoliths (using Breiby 1985, Härkönen 1986, and our own otolith collections), invertebrates by various hard parts (e.g. chitinous mandibles of polychaetes, carapaces/chelae of crabs). Otoliths of small cod Gadus morhua and saithe Pollachius virens are very similar in appearance and when difficult to distinguish were pooled as Gadidae. No attempt was made to pair otoliths, but the number from each species or group and the number of paired invertebrate organs (e.g. mandibles) in each pellet were counted. In an attempt to reduce biases induced by measuring partially digested otoliths (Jobling & Breiby 1986, Gales 1988, Johnstone et al. 1990) only otoliths which did not show signs of excessive digestion/wear were measured using a calibrated ocular grid in the microscope (R.T.B.), digital vernier calipers (J. L.) or mm graph paper under the microscope (N.R.). Minimal fish length was calculated from published data relating otolith size to fish

length (Jobling & Breiby 1986 for gadoids and sand eels *Ammodytes* spp., Härkönen 1986 for bull-rout *Myoxocephalus scorpius*). For small cod and saithe, the relationships between otolith length and standard length are very similar, and the mean of the 2 was used to estimate the standard length of unidentified gadoids (Table 1). Even if data are biased due to otolith erosion, direct comparisons of the size of fish caught by cormorants and shags can be made on the assumption that the degree of erosion is similar in these closely related species.

Results are presented numerically using the frequency of occurrence of each taxon (the number of pellets containing each taxon) and the numerical frequency of each taxon (the number of individuals of each taxon; Hyslop 1980). Although such a numerical presentation would overemphasize the number of prey items containing hard parts regurgitated in the pellets (e.g. otoliths and polychaete mandibles) and underestimate the number of possible soft-bodied animals which would be nearly totally digested, e.g. crustaceans (Johnstone et al. 1990), previous studies of whole stomachs or stomach regurgitations all show a predominance of fish in both shags and cormorants (Steven 1933, Lumsden & Haddow 1946, Madsen & Spärck 1950, van Dobben 1952, Pearson 1968, West et al. 1975, Ross 1976). Bounded by limitations of differential erosion and digestion of otoliths according to species and original size (Ross 1976, Duffy & Laurenson 1983, Johnstone et al. 1990), pellet analyses yield useful indications of dietary differences among colonies and species.

Assuming that the degree of erosion and loss of otoliths were the same in both species, such that absolute values for each species or locality may be misleading, a comparison of the relative values can be justified, e.g. through calculation of Morisita's index of diet overlap (Horn 1966, Diamond 1983). Our analysis was based on the percentage by number of each fish family (Level 3 of Diamond 1983) and of the classes Polychaeta, Crustacea and Echinoidea. Similarly, Shannon-Weaver diversity indices (Tramer 1969) were also calculated for each locality at the family level. Molluscs were excluded from both sets of calculations (see 'Results'). All statistical tests were carried out using MINITAB statistical package (Ryan et al. 1985).

# RESULTS

Totals of 6184 and 1635 identifiable animal body parts were isolated from 204 shag and ca 100 cormorant pellets, respectively. Although overlap indices comparing the Ferkinstadøyene samples with other Rogaland samples were low (0.66 to 0.73) due to the relatively high frequency (41%) of sand eels, compared to 1 to 6% in the other colonies, all Rogaland shag samples, and also the East Finnmark cormorant samples, were pooled due to small sample size from individual localities. There was no apparent seasonal variation in shag diet composition on Bleiksøy between May and August 1986 (overlap indices = 0.95 to 0.99); these data were also pooled.

### **Diet composition**

Fish were the most important prey of both species but more benthic fauna including relatively large numbers of molluscs and crabs were found in cormorant pellets (Tables 2 to 5). Whether the molluscs were eaten directly by the cormorants or whether they were from the diet of e.g. the gadoids is uncertain. *Helcion pellucidum*, for example, are small (< 1 cm) limpets which live firmly attached to *Laminaria* spp. and are a common prey for small coastal cod (W. Vader unpubl.). It is thus likely that they were a by-product of gadoid prey. In our analyses we assumed that molluscs were not eaten directly by shags or cormorants. In the Hovsflesa samples, the crabs were almost completely articulated and so large (carapace width 10 to 36 mm) that it is probable that they were avian prey.

Of the 5657 otoliths from shag pellets, only 121 (2.1%) were too eroded for identification, whereas 58 (5.1%) of the 1139 otoliths from cormorant pellets were unidentifiable. Otoliths from 11 families of fish were identified, but gadoids dominated the samples from both species (Figs. 2 and 3). The gadid otoliths we could identify suggested a dominance of saithe in the shag samples from Bleiksøy and the cormorant samples from Hovsflesa and Vikna, and of cod in the Munkholmen and East Finnmark samples. Otoliths of 2 large (ca 35 cm) haddock *Melanogrammus aeglefinus* were also

Table 1. Linear relationships between otolith length (OL) and standard fish length (SL)

Species	Equation	Source
Cod <i>Gadus morhua</i>	SL = 0.41 + 22.44OL	Jobling & Breiby (1986)
Saithe Pollachius virens	SL = -4.24 + 23.5OL	Jobling & Breiby (1986)
Gadid = (cod + saithe)/2	SL = -1.68 + 22.9OL	•
Sand eel Ammodytes tobianus	SL = 14.93 + 50.81OL	Jobling & Breiby (1986)
Bull-rout Myoxocephalus scorpius	SL = -9.95 + 34.8OL	Härkönen (1986)

Table 2. *Phalacrocorax aristotelis*. Frequency of occurrence (no. of pellets containing each item) of food items in shag pellets at Hornøy (1989), Bleiksøy (1985, 1986) and Rogaland (1988)

	Hornøy	Blei 1985	ksøy 1986	Rogaland	
No. of pellets	26	42	79	57	
Clupeidae (unident.)	0	0	4	1	
Mallotus villosus	1	0	2	0	
Myctophidae Benthosema glaciale	0	1	0	0	
Gadidae (unident.)	20	39	71	41	
Trisopterus sp.	0	0	0	17	
Labridae (unident.)	0	0	0	36	
Ammodytes sp.	16	10	27	12	
Anarhichas sp. Scorpaenidae	1	0	0	0	
Sebastes sp. Cottidae	6	1	5	6	
Mvoxocephalus scorpius	0	9	32	0	
Pleuronectidae (unident.)	0	3	3	0	
Unident. fish	2	9	13	20	
Polychaetes					
Nereis sp.	0	25	21	21	
Polynoidae	1	2	6	0	
Isopoda	1	0	0	0	
Decapoda	4	0	17	22	
Gastropoda	0	0	3	0	

found in the Munkholmen samples. Another apparently important prey of both shags and cormorants was sand eel *Ammodytes* sp. which was numerous at all shag localities and in cormorant samples from East Finnmark (Figs. 2 and 3). Mandibles of polychaetes (mostly *Nereis*, but also some Polynoidae) were also frequent in most samples (Tables 2 to 5). Although they too could have originated from the stomachs of fish eaten by birds, it is also possible that they were caught during their periodic pelagic swarming phase (Hartmann-Schröder 1971). This speculation is strengthened by the fact that polychaetes were common in the cormorant samples from Hovsflesa in 1985 but were completely absent in 1986 in an otherwise similar food spectrum (Tables 4 and 5, Fig. 3)

All indices of dietary overlap among all shag localities were relatively high (Table 6) suggesting a narrow and consistent diet. Gadoids and sand eels together dominated at all localities although shags relied more heavily on sand eels on Hornøy than at other colonies (Fig. 2). Bull-rout *Myoxocephalus scorpius* was found on Bleiksøy only, while *Trisopterus* sp. and wrasse (Labridae) only occurred in the Rogaland samples. Of the crustaceans recorded, the Hornøy and Rogaland samples contained remains of prawns (Natantia)/euphausiids while those from Bleiksøy 1986 were of crabs (Brachyura and Anomura).

Of identified prey in all the cormorant samples, 23 to 70 % were gadoids, the highest values being found in Trøndelag (Fig. 3). Sand eels and capelin were only found in East Finnmark where redfish *Sebastes* sp. and salmonids were also common. There was a tendency for cormorants in East Finnmark to have a more varied diet (5 fish species each contributing to > 5 % of diet) than at the other localities (Fig. 3) resulting in the highest diversity index and the lowest mean overlap index for any one locality (Table 6). For shags, diet breadth increased from north to south (Table 6).

## Size of fish eaten

Cormorants took larger gadoids than shags (Fig. 4, Table 7; Mann-Whitney U =  $5.9 \times 10^{6}$ , p < 0.001). There was a remarkable correspondence between the bimodal length frequency distribution of fish caught by shags and the known sizes of juvenile saithe and cod from northern waters (Fig. 5). This, and the minimal erosion of cod otoliths recorded in shags by Johnstone et al. (1990) suggest that, in the case of gadoids at least, our estimations of fish size are reasonable. If so, it seems that shags prey mainly on 0- and I-group fish, while cormorants also catch II-group fish. Few 0-group gadoids were recorded for either species in East Finnmark. A detailed breakdown of the Bleiksøy data revealed a shift in year-class predominance (from 0 in 1985 to I in 1986; Table 7) which may be related to a lower spawning success of saithe in 1986 (Nedreaas & Smedstad 1987, R.T.B. unpubl.).

Cormorants also took larger *Myoxocephalus scorpius* than shags in the Vesterålen/Lofoten region (Bleiksøy/ Hovsflesa, Mann-Whitney U =  $1.1 \times 10^4$ , p < 0.001), but smaller sand eels in East Finnmark (Fig. 6, Table 7; Mann-Whitney U = 3672, p < 0.001).

There is a good probability that many of the sand eel otoliths were indeed eroded before regurgitation (Johnstone et al. 1990), yet the length frequency distributions of sand eels caught at the 3 shag localities were all similar (median 100 to 130 mm, range ca 80 to 160 mm; Table 7, Fig. 6) and fell within the approximate size range of I- to IV-group fish (Reay 1970).

#### Harvest of gadoids

The daily energy expenditure (DEE) of shags and cormorants can be calculated on the assumption that free-living birds require ca  $3 \times$  basal metabolic rate (BMR) (Birt-Friesen et al. 1989, Furness 1990). BMR

	Hornøy	Blei	ksøv	Rogaland
		1985	1986	Ū.
Fish otoliths				
Clupeidae (unident.)	0	0	7	2
Osmeridae				
Mallotus villosus	1	0	3	0
Myctophidae				
Benthosema glaciale	0	2	0	0
Gadidae (unident.)	323	1884	1120	401
<i>Trisopterus</i> sp.	0	0	0	102
Labridae (unident.)	0	0	0	205
Ammodytidae				
Ammodytes sp.	450	126	529	152
Anarhichadidae				
Anarhichas sp.	2	0	0	0
Scorpaenidae				
Sebastes sp.	13	3	34	17
Cottidae				
Myoxocephalus scorpius	0	14	141	0
Pleuronectidae (unident.)	0	3	4	0
Unident. fish	2	12	44	63
Other				
Polychaetes				
Nereis sp.	0	273	92	50
Polynoidae	3	8	44	0
Iconada	n	0	0	0
Isopoua Decemente	2	0	22	20
Decahona	5	U	22	20
Gastropoda	0	0	6	0
Totals	801	2325	2044	1014

Table 3. Phalacrocorax aristotelis. Numerical frequency of food remains in shag pellets at Hornøy (1989), Bleiksøy (1985, 1986)and Rogaland (1988)

was calculated from the allometric equation for seabirds at any latitude,  $BMR = 433.5 \text{ m}^{0.734}$  where m = body weight in kg (Gabrielsen et al. in press). Body weights (shags = 1800 g, cormorants = 3250 g) were taken from own unpublished data and Cramp & Simmons (1977). Quantities of fish consumed were calculated from DEE using a value of 85 % for assimilation efficiency (Dunn 1975) and a calorific value for gadoids and other small fish of 5.5 kJ  $g^{-1}$  (Barrett et al. 1987, unpubl.). Using these relationships, the daily food consumptions of shags and Cormorants are calculated to be 430 and 661 g fish repectively. These weights are equivalent to 24 and 20 % of body weight respectively, and similar to the 22% reached for freeliving shags calculated from Furness (1990). Because metabolic rate increases with activity (Birt-Friesen et al. 1989), the lower values (16 to 18%) recorded for captive shags and white-breasted cormorants Phalacrocorax lucida by Johnstone et al. (1990) and Junor (1972) are probably a result of constraint.

Based on breeding populations of 30 000 shags and 42 000 cormorants, the monthly harvest by breeding

adults will thus be ca 400 tonnes (shag) and 850 tonnes (cormorant), yielding totals of ca 1600 and 3400 tonnes respectively during the main breeding season (April to July). Assuming the proportion of gadoids taken is ca 50% (this study – allowing for the more rapid digestion of e.g. sand eel otoliths) and that it is the same throughout the breeding season, this gives a total consumption of gadoids of ca 6000 tonnes by adults of both species (including breeders and nonbreeders; latter based on population parameters given in Table 8 and assuming immature birds have the same diet as adults) during the breeding season.

An alternative calculation can be based on the number of gadoid otoliths found in each pellet (ca 20 for shags, 10 for cormorants; Tables 1 to 4), the size (and hence weight using a condition factor = 1) of fish from each locality and the assumptions that (1) each bird produces one pellet per day, (2) there is little erosion of gadoid otoliths and (3) that only 67 % of the gadoid otoliths are regurgitated in the pellets (Jobling & Breiby 1986, Johnstone et al. 1990). This results in a daily consumption of 15 gadoids weighing 0.17 kg by

	Hovs	flesa	Munkholmen	Vikna	
	1985	1986			
No. of pellets	17	21	16	13	
Clupeidae					
Clupea harengus	0	1	0	0	
Salmonidae					
Salmo sp.	0	0	0	1	
Gadidae (unident.)	14	17	9	13	
Gadus morhua	0	0	13	0	
Melanogrammus aeglefinus	0	1	2	0	
Pollachius virens	0	0	1	0	
Trisopterus sp.	0	0	2	0	
Labridae (unident.)	0	0	1	0	
Anarhichadidae					
Anarhichas sp.	2	2	0	0	
Scorpaenidae					
Sebastes sp.	1	3	0	0	
Cottidae					
Myoxocephalus scorpius	7	5	0	1	
Pleuronectidae (unident.)	4	2	4	2	
Unident. fish	3	3	1	1	
Polychaetes	10	0	7	1	
sopoda	0	1	0	0	
Natantia	0	1	0	0	
Hyas spp.	9	5	0	0	
Pagurus bernhardus	1	8	0	0	
Unident. crab	2	1	7	4	
Loricata	1	2	0	0	
Gastropoda	6	11	5	3	
Helcion pellucidum	4	2	0	0	
Lamellibranchia	1	2	3	5	
Echinoidea	5	5	0	3	

 Table 4. Phalacrocorax carbo. Frequency of occurrence of food items in cormorant pellets at Hovsflesa (1985, 1986), Munkholmen (1986) and Vikna (1987)

shags and 7.5 gadoids weighing 0.33 kg by cormorants, or 600 and 1700 tonnes during the same 4 mo respectively. Again assuming immature birds have the same diet, their consumption is calculated to ca 4000 tonnes. Either way, it seem reasonable to suggest that Norwegian shags and cormorants consume on the order of 6000 tonnes of 0-, I- and II-group cod or saithe during the breeding season.

In actual numbers, breeding shags may take as many as  $55 \times 10^6$  and cormorants  $40 \times 10^6$  gadoids per season. Estimates based on Figs. 4 and 5 show that of the gadoids eaten by shags, 65% are 0-group and 34% Igroup. For cormorants, 38% are 0-group, 50% I-group and 11% II-group giving a total harvest of  $50 \times 10^6$  0group,  $40 \times 10^6$  I-group and  $4 \times 10^6$  II-group gadoids by both species. Including immature birds would raise these totals to 144, 110 and  $12 \times 10^6$  respectively. Given the close agreement of the results of both biomass calculations and that shags and cormorants are generally heavy predators on gadoids, these values are probably in the correct order of magnitude.

# DISCUSSION

Recognizing the limitations of the pellet analyses used, shags and cormorants must rely heavily on small fish for food in summer and autumn throughout their range in Norway. Although the numbers of polychaetes found in the cormorant pellets in Lofoten and Trøndelag were relatively high, their contribution to the species' diet as it appears when expressed numerically in Fig. 3 is exaggerated. If it was expressed gravimetrically they would contribute little to overall diet. A single polychaete weighs ca 1 to 2 g compared to a median gadoid of 150 mm length and a biomass of ca 30 g (based on a fish with a condition factor (CF) of 1, CF imesmass =  $l^3/100$  where l = length in cm). Polychaetes are normally sedentary with short, periodic swarming phases during the spawning season (Hartmann-Schröder 1971) such that they are often not available to pelagic predators. Furthermore, when they do swarm they do so in such large numbers that they could contribute an unrealistically high proportion of

Fish otoliths         1963         1960           Clupeidae         0         0         2         0           Salmonidae         39         0         0         0         0           Salmo sp.         39         0         0         0         0         0           Gadidae (unident.)         0         104         156         26         9         9           Gadidae (unident.)         0         0         3         2         9         14         14         14         14         14         15         14         14         14         14         14         14         15         14         14         14         14         14         14         15         14         15         15         15         15         14         15         15         15         14         15         14         15         15	Vikna
Fish otoliths         Clupea harengus       0       0       2       0         Salmonidae         Salmo sp.       39       0       0       0         Osmeridae         Mallotus villosus       103       0       0       0       0         Gadus morhua       155       0       0       0       Gadus morhua       155       0       0       0       0       0       0       0       0       0       1         Gadus morhua       155       0       0       0       0       1         Gadus morhua       15       0       0       0       1         Gadus morhua       15       0       0       0       1         Colspan="2">Colspan="2">Colspan="2">Colspan="2">Colspan="2">Colspan="2">Colspan="2">Colspan="2"Colspan="2"Colspan="2"Colspan="2"Colspan="2"Colspan="2"Colspan="2"Colspan="2"Colspan="2"Colspan="2"Colspan="2"Colspan="2"Colspan="2"C	
Clupeidae       0       0       2       0         Salmonidae       39       0       0       0         Osmeridae        0       0       0         Mallotus villosus       103       0       0       0         Gadidae (unident.)       0       104       156       26       9         Gadidae (unident.)       0       104       156       26       9         Melanogrammus aeglefinus       0       0       3       2       9         Melanogrammus aeglefinus       0       0       3       2       9         Mallotus vitens       2       0       0       1       1       1         Ammodytidae       0       0       0       1       1       1       1         Anarhichadidae       -       -       -       -       1 <td></td>	
Clupea harengus         0         0         2         0           Salmonidae	
Salmonidae       39       0       0       0         Osmeridae $Mallotus villosus$ 103       0       0       0         Gadidae (unident.)       0       104       156       26       9         Gadus morhua       155       0       0       92       9         Melanogrammus aeglefinus       0       0       3       2       9         Pollachius virens       2       0       0       1       1         Trisopterus sp.       0       0       0       1       1         Ammodytidae       -       -       -       -       -         Anarhichadidae       -       -       -       -       -       -         Sebastes sp.       59       2       7       0       - <t< td=""><td>0</td></t<>	0
Salmo sp.       39       0       0       0         Osmeridae	
Osmeridae       Mallotus villosus       103       0       0       0         Gadidae (unident.)       0       104       156       26       9         Gadus morhua       155       0       0       92         Melanogrammus aeglefinus       0       0       3       2         Pollachius virens       2       0       0       1         Trisopterus sp.       0       0       0       3         Labridae (unident.)       0       0       0       1         Ammodytidae       -       -       -       -         Anmodytes sp.       123       0       0       0       -         Scorpaenidae       -       -       -       -       -         Scorpaenidae       -	2
Mallotus villosus       103       0       0       0         Gadidae (unident.)       0       104       156       26       9         Gadus morhua       155       0       0       92       9         Melanogrammus aeglefinus       0       0       3       2       9         Pollachius virens       2       0       0       1       9         Trisopterus sp.       0       0       0       3       2         Ammodytidae	
Gadidae (unident.)       0       104       156       26       9         Gadus morhua       155       0       0       92       9         Melanogrammus aeglefinus       0       0       3       2       9         Pollachius virens       2       0       0       1       7         Pollachius virens       2       0       0       1       7         Itabridae (unident.)       0       0       0       3       2         Ammodytidae	0
Gadus morhua       155       0       0       92         Melanogrammus aeglefinus       0       0       3       2         Pollachius virens       2       0       0       1         Trisopterus sp.       0       0       0       3         Labridae (unident.)       0       0       0       1         Ammodytidae $3$ 2       0       0         Anarhichadidae $3$ 2       0       0         Anarhichas sp.       0       3       2       0         Sebastes sp.       59       2       7       0         Cottidae $32$ 17       5       2         Myoxocephalus scorpius       21       29       14       0         Pleuronectidae (unident.)       0       5       4       5         Unident. otoliths       32       17       5       2         Other $7$ $9$ $9$ $16$ $0$ Isopoda $0$ $0$ $1$ $0$ Natantia $0$ $11$ $0$ Hyas spp. $0$ $15$ $15$ $15$	93
Melanogrammus aeglefinus       0       0       3       2         Pollachius virens       2       0       0       1         Trisopterus sp.       0       0       0       3         Labridae (unident.)       0       0       0       1         Ammodytidae	0
Pollachius virens       2       0       0       1         Trisopterus sp.       0       0       0       0       3         Labridae (unident.)       0       0       0       0       1         Ammodytidae	0
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Polychaete jaws         0         86         0         15           Isopoda         0         0         1         0           Natantia         0         0         1         0           Hyas spp.         0         19         8         0	
Isopoda         0         0         1         0           Natantia         0         0         1         0           Hyas spp.         0         19         8         0	1
Natantia         0         0         1         0           Hyas spp.         0         19         8         0	0
Hyas spp.         0         19         8         0           Present hamber         0         1         15         0	0
	0
Paqurus bernnardus 0 1 15 0	0
Unident. crab 0 2 1 7	4
Loricata 0 1 2 0	0
Gastropoda 0 38 20 5 2	25
Helcion pellucidum 0 135 60 0	0
Lamellibranchia 0 1 3 18	9
Echinoidea 0 6 9 0	3
Totals 534 449 313 177 14	42

 Table 5. Phalacrocorax carbo. Numerical frequency of food items in cormorant pellets at East Finnmark (1989), Hovsflesa (1985, 1986), Munkholmen (1986) and Vikna (1987)

diet over a period of only a few days. That our single day collecting trips at Cormorant colonies only sometimes coincided with such swarming periods may explain the absence of polychaetes in the samples from Hovsflesa in 1986 and from East Finnmark in 1989. During the same period that cormorant pellets were sampled on Hovsflesa in 1986, only 10 polychaete mandibles (of a total of 136 collected that year; Table 3) were found on Bleiksøy (on 6 to 15 July 1986) in 4 of 18 shag pellets. It seems that cormorants rely heavily on gadoids in Lofoten and Trøndelag, while in Finnmark other fish species (especially capelin and sand eels) are equally important dietary items (Fig. 3) resulting in the highest diversity index of the localities studied (Table 6).

The importance of gadoids in the diet of shags and

cormorants in Norway reflects the summer distribution of small cod and saithe. While juvenile (0- and I-group) saithe remain inshore all year, immature coastal cod move into shallow, coastal feeding areas in summer (Bergstad et al. 1987), and thus enter the normal foraging range limits of both avian species (20 to 50 km; Cramp & Simmons 1977). Furthermore, while all ageclasses of both species may be present in large numbers along the west and northwest coasts of Norway (where the main spawning areas occur; Bergstad et al. 1987), it is likely that fewer young fish will be available in East Finnmark where coastal spawning populations are much smaller. This would explain the paucity of younger stages in the diets of shags and cormorants in this region (Fig. 4). Wrasse have a similar seasonal



Fig. 2. *Phalacrocorax aristotelis.* Proportion (by number) of the most common prey eaten by shags in Norway. For explanation of symbols, see Fig. 3

migration, moving into coastal waters from offshore wintering areas in summer (Pethon 1985), but because their northern limit of distribution is western Norway, they only appear in Rogaland samples. Similarly capelin is a cold water species whose distribution is confined to northern waters, and it is rarely found in seabird diets south of Finnmark (Barrett et al. 1987, R. T. B. unpubl.).

In East Finnmark, capelin is abundant and is an important prey for nearly all seabirds breeding in the





Fig. 3. *Phalacrocorax carbo. Proportion* (by number) of the most common prey eaten by cormorants in Norway

 

 Table 6. Phalacrocorax aristotelis and P. carbo. Intercolony overlap (Morisita's index) in and diversity (Shannon-Weaver index) of the diets of Norwegian cormorants and shags

Cormorant		1	Morisita's index	Morisita's index						
	Finnm	Hov 85	Hov 86	Munk	Vikna	index				
East Finnmark		0.51	0.61	0.57	0.56	0.70				
Hovsflesa 1985			0.74	0.76	0.68	0.63				
Hovsflesa 1986				0.97	0.93	0.46				
Munkholmen					0.99	0.30				
Vikna						0.25				
Mean	0.56	0.67	0.81	0.81	0.79	0.47				
Overall overlap mean. 0 72										
Shag		M	orisıta's index			SW.				
	Hornøy	Bl 85	Bl	86	Rog	index				
Hornøy		0.62	0.	86	0.73	0.37				
Bleiksøy 1985			0.	89	0.86	0.27				
Bleiksøy 1986					0.91	0.52				
Rogaland						0.56				
Mean Overall overlap mean: 0.81	0.74	0.79	0.	87	0.83	0.43				





region (Furness & Barrett 1985, Barrett & Furness 1990). While capelin is eaten by cormorants (this study), it has never appeared in shag samples (includ-

Table 7. Median lengths (mm) of the commonest fish caught by shags and cormorants in Norway (no. of otoliths in parentheses)

	Gadi	dae	Ammo	odytesª	M. sco	orpiusª
Cormorant						
East Finnmark	170	(152)	83	(51)		
Hovsflesa 1985	146	(98)			104	(42)
Hovsflesa 1986	180	(154)				
Vikna	159	(91)				
Munkholmen	159	(120)				
Overall median	158	(615)				
Shag						
Hornøy	143	(276)	103	(247)		
Bleiksøy 1985	57 (1	588)	127	(130)		
Bleiksøy 1986	133 (1	000)	122	(294)	86	(138)
Rogaland	58	(404)	111	(157)		
Overall median	90 (3	268)	111	(828)		
° Probable under	estimat	es; se	e 'Disci	ussion'		









ing adult and chick regurgitations collected on Hornøy since 1980; Furness & Barrett 1985, Barrett et al. 1986, this study). Capelin shoal throughout the water column and are caught close to Hornøy by deep divers (guillemots *Uria* spp.), shallow divers (puffins *Fratercula arctica*, black guillemots *Cepphus grylle*) and surface feeders (kittiwakes *Rissa tridactyla*, gulls Laridae (Fur-

		Shag	Cormorant	Source
No. breeding adul	ts	30 000	42 000	Røv (1984), Røv & Strann (1986)
Fledging rate (chicks pair <sup>-1</sup> yr <sup>-1</sup>	<sup>1</sup> )	2	2.5	Barrett et al. (1986), Røv & Strann (1986)
Annual survival	1st yr	50	50 )	
rates (%)	2nd yr	75	65	Cramp & Simmons (1977), Potts et al.
	3rd yr	80	65	(1980), Aebischer (1986)
	4+ yr	80	65)	
Age at 1st breedin	ıg	3-4	4-5	

 Table 8. Phalacrocorax aristotelis and P. carbo. Population parameters of shags and cormorants used to calculate numbers of individuals in Norway in the breeding season

ness & Barrett 1985, Barrett & Furness 1990) and should thus be available to shags. Capelin otoliths are hyaline and therefore more rapidly digested than those of gadoids (Jobling & Breiby 1986), but it is unlikely that they would be totally digested by shags and not by cormorants.

Consistent with earlier studies (summarized in Cramp & Simmons 1977), this study suggests that Norwegian shags have a more restricted diet breadth (a slightly lower mean diversity index) than cormorants (Tables 6 and 9) and that cormorants feed more on or near the seabed than shags. Gadoids and sand eels appeared to be shaqs' commonest prey throughout their range, while cormorants, at least in East Finnmark, tended to be more opportunistic. Overlap indices between species were however higher in East Finnmark and in the Lofoten/Vesterålen area than from areas in sympatry in Great Britain (Table 9). Three of the 4 British studies were carried out in estuarine habitats, and in all 4 cormorants ate a higher proportion of flatfish and other benthic organisms which resulted in lower overlap indices. Unlike these and several other studies where flatfish were well represented in cormorant diets (Steven 1933, Pearson 1968, Mills 1969, Rae 1969, Cramp & Simmons 1977, Pilon et al. 1983, Birt et al. 1987), few flatfish were recorded in this study. Diet breadth was also greater in Bitain (Table 9), a direct reflection of the greater prey diversity in the habitats studied. Our data come from more exposed and rocky habitats unfavourable to flatfish but where the low prey diversity was offset by the abundance of the most important prey (gadoids and sand eels). This plus the spatial separation of the localities compared suggest little competition between shags and cormorants. This conclusion concurs with that of Pilon et al. (1983) whose data also reveal high overlap indices (0.87 to 0.89) and low effective competition between sympatric Phalacrocorax carbo and P. auritus in Quebec, Canada, where the main prey were also abundant. A similar analysis of Ross' (1976) data on the same species in Nova Scotia shows an overlap more similar to the British data (0.34

(nestling regurgitates by weight) -0.64 (adult pellets by number)) and can be explained by different foraging habitats around the localities studied. Similarly in southwestern North America, the overlap indices between 3 *Phalacrocorax* species were low (0.1 to 0.5), again as a direct result of feeding habitat diversity (Ainley et al. 1981).

### Implications for gadoid stock recruitment

Most of the gadoids caught by shags and cormorants are probably saithe. In Norway, cod spawn from February to April in coastal waters mainly from Lofoten to West Finnmark, but also to a lesser extent off the southwest coast (Bergstad et al. 1987). By June–July most postlarvae and juveniles have drifted northwards to the Barents Sea where they remain until mature, although some remain in the northern fjords and over banks. Saithe also spawn early, mainly in February. The main spawning areas are further south than those of the cod (from Møre to Lofoten), and in contrast to cod fry which have an oceanic and coastal drift, most saithe fry soon move ashore to a littoral habitats and remain near the coast until 3 yr old (Bergstad et al. 1987).

There is no human exploitation of the youngest stages of gadoids in Nowegian waters. Though there are no biomass data for these fish, results of annual surveys by the Norwegian Institute of Marine Research (Bergen) have generated numerical estimates of these young fish available to potential predators along the coast and in the Barents Sea (Tables 10 and 11). Apart from 2 strong year classes of 0-group fish (in 1983 and 1985, Anonymous 1989, S. Sundby pers. comm.), the level of production of 0-group cod has been poor (< 1000  $\times$   $10^{6}$  ind.  $\rm yr^{-1}$ ) since 1976. Between 1946 and 1981, the mean year-class strength of I-group saithe was  $263 \times 10^6$  individuals (SD =  $110.5 \times 10^6$ , range 69 to  $464 \times 10^{6}$ ) yr<sup>-1</sup> (from Jakobsen 1987). Since 1985 however, saithe recruitment has dropped by ca 40 %  $yr^{-1}$  (Table 11). According to the values presented

Area	M. index	SW	/. index	Source
		Shag	Cormorant	
East Finnmark	0.76)			
Hovsflesa/Bleiksøy 1985	0.76 }			This study
Hovsflesa/Bleiksøy 1986	0.88 )			
Farne Islands	0.50	0.34	0.78	Pearson (1968)
Cornwall	0.11	0.56	0.51	Lack (1945)
River Dee	0.55	0.73	0.75	Rae (1969)
Angus/Kincardineshire	0.24	0.58	0.78	Rae (1969)

 Table 9. Phalacrocorax aristotelis and P. carbo. Interspecies overlap (Morisita's index) in areas of sympatry and diversity (Shannon-Weaver index) of the diet of Norwegian and British cormorants and shags

Table 10. Gadus morhua. Numbers (×10<sup>6</sup>) of young cod along the coast of Norway and in the Barents Sea in poor, average and strong year classes. (Based on back-calculations from abundance estimates of III-group fish. From Hylen 1984)

Age		Size of year clas	s
group	Poor	Average	Strong
0	300-600	1100-2200	2900-5800
I	300-500	1000-1900	2700-4900
II	200-300	800-1100	2200-3000

Table 11. Population indices (0-group saithe) and absolute numbers ( $\times 10^6$ ) of I- and II-group saithe and cod along the Norwegian coast and in the Barents Sea. (Based on 0-group surveys and VPA-analyses. From Mehl et al. 1988, Anon. 1990, Nedreaas pers. comm.)

		Sp			
	1984	1985	1986	1987	1988
0	_	828	545	285	165
Ι	-	225	99	161	(200)
Π	-	262	184	81	
Ι	1091	258	196	286	_
II	557	910	215	163	238
Ш	386	464	758	179	136
	O I II II III	1984 0 – I – II – I 1091 II 557 III 386	Sp 1984 1985 0 – 828 I – 225 II – 262 I 1091 258 II 557 910 III 386 464	Spawning y 1984 1985 1986 0 – 828 545 I – 225 99 II – 262 184 I 1091 258 196 II 557 910 215 III 386 464 758	Spawning year           1984         1985         1986         1987           0         -         828         545         285           I         -         225         99         161           II         -         262         184         81           I         1091         258         196         286           II         557         910         215         163           III         386         464         758         179

above, a consumption of 110 million I-group fish by shags and cormorants during the 4 summer months would alone be equivalent to > 20 % of the total annual stock of I-group saithe and cod in 1985 to 1988 (range 295 to 483 million fish, Table 11). This estimate is unquestionably too high and potential inaccuracies in our data sets and those of the Norwegian Institute of Marine Research should be considered. For example, the estimation of stock sizes of the youngest classes of fish using single species VPA-analyses are often unreliable. Recent studies (Hildén 1988a) indicate that the mortality factors used for small fish in such analyses are not only generally too low, but also very sensitive such that small adjustments can result in large changes in the numbers of small fish available to predators. Furthermore, our diet data set is not neccessarily representative for the whole coast of Norway, nor do we have data for non-breeding birds. Nevertheless it seems that irrespective of prey species, the numbers of fish eaten by shags and cormorants are potentially high compared to the numbers apparently available and that predation by these species could affect the recruitment of young fish into 2 important commercial fisheries during years of low stock size.

The situation has recently been exacerbated by decreases in important prey species of the cod (capelin, prawn, herring) in 1986/87 resulting in considerable cannibalism of the youngest stages of cod spawned since 1984 such that even the recruitment of the strong 1984 to 1986 year-classes has been severely limited (S. Mehl pers. comm.). Levels of cannibalism (Mehl 1989) have been on the same order of magnitude as the apparent predation by shags and cormorants (Table 12). Keeping in mind that our estimations of predation only considered the 4 summer months (ringing data shows that both species are resident along the coast throughout the year (Myrberget 1973, Johansen 1975, Galbraith et al. 1986, K.-B. Strann pers. comm., N. R. & R. T. B. unpubl.), and even if they are overestimated by an order of magnitude, it seems possible that predation by shags and cormorants could be a factor limiting the

Table 12. The Northeast Arctic cod stock's consumption of young cod during the summer and autumn in tonnes  $(\times 10^6)$  and numbers  $(\times 10^6)$ . (From Mehl 1989)

Age		Biomass			Numbers		
group	1984	1985	1986	1984	1985	1986	
0	_	3	0.2	-	2506	85	
Ι	10	5	7	108	125	344	
II	1	11	23	13	41	158	
III	+	-	36	+	-	137	

build up of these 2 important fish stocks in the Northeast Atlantic. However, problems related to the systematic quantification of the natural mortality of fish attributable to other predators and of other factors regulating the populations of these early life stages of gadoid fish need to be resolved for managers (Hildén 1988b, Lapointe et al. 1989). More detailed studies of the species composition of gadoids, of possible seasonal and age-related variations in diets of shags and cormorants, their daily energy intake and of avian responses to changes in prey abundance are also required to further quantify any effects of predation by these birds. This study raises the importance of the consideration of predation by seabirds in fisheries multispecies modelling. It is also in sharp contrast with previous studies which all concluded that neither shags nor cormorants had any significant effect on commercial species. It is worth noting that cormorants and shags might also exert a favourable influence on fish populations by preying on heavily parasitized fish and by eating species that prey on commercially exploited fish (van Doben 1952).

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