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Utilization of discarded fish by scavenging seabirds behind whitefish trawlers in Shetland

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(With 3 figures in the text)

Although the availability of discarded fish from trawlers has been suggested as a cause of population increases of scavenging seabirds in the British Isles during this century, the study described here provides the first quantitative data on the utilization of discard fish by different seabird species. Around Shetland in summers 1984 and 1985, great black-backed gulls, gannets and great skuas obtained most discard fish. Discards were predominantly whiting and haddock 24–32 cm in length. Great skuas were highly selective, taking mainly the smaller whiting. Although great skuas frequently attempted to rob other birds, they had difficulty in handling larger discard fish and as a result had more fish stolen from them than they stole. Great black-backed gulls and gannets were less selective, being able to swallow a wider range of fish species and sizes, and great black-backed gulls stole many more fish than they had stolen from them. On average, larger scavenging species swallowed larger fish, and dropped less. The proportion of discards dropped increased with fish size. Haddock and whiting were mainly consumed but many gurnards and most flatfish were rejected by seabirds and allowed to sink. The large size of discards from Shetland trawlers puts smaller scavenging seabirds (herring and lesser black-backed gulls, great skuas) at a competitive disadvantage; great black-backed gulls and gannets exploit discards most effectively. Current changes to net-mesh size will accentuate the competitive advantage of these larger birds.

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Introduction

During the 20th century, the populations of most seabirds in Britain have increased dramatically. This has been particularly marked for species which, from time to time obtain some of their food by scavenging, such as great skua *Catharacta skua*, fulmar *Fulmarus glacialis*, herring gull *Larus argentatus* and gannet *Sula bassana* (Cramp, Bourne & Saunders, 1974). The causes of these increases have been, and remain, a matter of considerable dispute (Furness & Monaghan, 1987). Reduced human persecution has undoubtedly been important, but many authors have attributed the increase primarily to the availability of novel food supplies as a consequence of man's activities. Fisher (1952) claimed, without quantitative data on dietary composition, that offal from trawlers had supported the spread and increase of the fulmar. Furness & Hislop (1981) argued from a study of diet composition but without observations of foraging ecology that the availability of discards may have been an important factor in allowing the great skua population in Orkney and Shetland to increase at an average rate of 7% per annum between 1900 and 1977. However, the quality and quantity of food made available to scavenging seabirds by the fishing industry and the ways in which this is exploited by seabirds has not previously been studied. Lack of information on the utilization of discards by seabirds has prevented clear understanding of the importance of this food supply in their ecology and population dynamics.

Furness, Hudson & Ensor (In press) estimated that the quantity of fish discarded from whitefish trawlers in the northern sector of the North Sea could support the food needs throughout the year of up to 300,000 seabirds, representing perhaps 5–10% of the seabirds in that sector. That calculation implies that discards may indeed be an important influence in the ecology of scavenging seabirds. The aim of this paper is to present quantitative information on the kinds of fish discards made available to seabirds around Shetland, and on the ability of different species to exploit this food supply.

Methods

During April–August 1984 and 1985, observations were conducted from whitefish trawlers around Shetland of seabirds feeding on discarded fish and offal. We define 'offal' as the livers and intestines of marketable fish that have been removed during fish sorting and cleaning operations and thrown overboard, and 'discards' as fish that are below the legal minimum size for market sale, too small to be considered by the fishermen to be worth landing for market, or species for which there is no demand, or fish that are in excess of the quotas to which individual boats are working. Thus, the proportion of the catch that is discarded varies according to the catch composition, current market demands, and the idiosyncrasies of particular fishing crews. Trawler trips were made principally from the west coast of Shetland, and were on small whitefish trawlers, of about 20–30 m length. Fishing was generally within 15–35 km of the coast.

In 1985, random samples of fish being discarded by the fishermen were set aside and examined to determine the species composition and sizes of fish available for exploitation by seabirds. In total, 7605 fish were identified to species, their total length measured to the nearest cm and then discarded singly from the stern of the trawler. The measured discards were then watched and foraging attempts by scavenging seabirds recorded by video camera or by dictating into a tape recorder. The species of seabird, and where possible its age class, was recorded in each case, and the outcome of the feeding attempt was recorded, thus determining the selection of fish by different species and age classes of scavenging seabirds, and the frequency and outcome of interactions during feeding. Although initial observations were made by video recording seabirds feeding, it was found that data could be collected as reliably but much more easily by dictation into a pocket cassette recorder, and most observations were recorded by the latter method.

Nearly half of the fish that were experimentally discarded were seen to be swallowed by seabirds, but it often proved impossible to record the ultimate fate of individual discards. Sometimes the boat was moving so that the fish disappeared out of sight before its fate could be determined; other times the sea was choppy and the fish could not be kept in sight. On other occasions, birds flew away into the distance carrying the fish and it was not known whether the fish was swallowed, dropped, or stolen by another bird. Kleptoparasitism, the stealing of a fish by one bird from another, occurred commonly. A few fish were ignored by seabirds, often because they were too large for the birds to swallow or were of unpopular fish species. Video film analysis showed that seabirds would approach such fish but would turn away after a close inspection. Although the smaller scavenging seabirds appeared to do this most often, and particularly when the discard was a flatfish or an especially large roundfish, it proved difficult to define when a bird had begun to focus on a fish and when it aborted its approach, and so we decided not to try to analyse this aspect of the observations in a quantitative manner.

Some fish sank before being consumed, but less than 10% of fish were known not to have been swallowed by a bird, and it seems likely that at least half of the fish, where their fate could not be recorded, were swallowed.

Experimental discarding was performed during several hauls on each of 19 different fishing trips on a variety of boats. As a result of this data collection strategy, it is theoretically possible that spurious statistical associations could arise if a particular trip happened, by chance, to have involved, for example, unusually many herring gulls and unusually small fish. Such a problem is unlikely to arise where, as in our study, no one day of observations contributed more than 10% of the data. However, we carried out an analysis to check the validity of pooling observations between trips. Analysis of variance showed that fish length varied significantly between trips, although between trip variance was slight compared with total variance. However, ANOVA showed no significant difference in seabird species composition between trips, and covariance analysis showed no significant between-trip associations between fish length or species and seabird species composition, so that analysis of fish selection by particular seabirds can be performed on the pooled data set.

The extent to which fish were selected by virtue of their length, as well as their species, was determined by comparing the mean lengths of all haddock *Melanogrammus aeglefinus* and whiting *Merlangius merlangus* discarded with the mean lengths of fish that were seen to be swallowed, dropped or stolen by each age class and species of bird (where sample sizes permitted meaningful statistical comparison). The maximum lengths of fish taken by the different bird species were examined, and related to the sizes of fish discarded.

Following general practice with the use of chi-squared tests, we have omitted from analysis categories where expected frequencies were less than one and have ensured that no more than 20% of expected frequencies were less than five.

Results

Fish species and sizes discarded

Over 70% of all fish discarded were haddock and whiting. Flatfish comprised 15% of the discards and gurnards another 10%, while 2% consisted of cod *Gadus morrhua*, saithe *Pollachius virens* and Norway pout *Trisopterus esmarkii*. A further nine or ten species made up less than 1% of the total (Table I).

Haddock and whiting discards ranged in length from 14–39 cm, with median lengths of 28 and

TABLE I

Numbers and median lengths of fish of each species in a sample of fish discarded from whitefish trawlers around Shetland in summer 1985

Fish species	Number discarded	Percentage of total	Median length (cm)	Number known to be swallowed by seabirds	Percentage known to be swallowed
Haddock	2859	37·6	28	1691	59
Whiting	2589	34·0	29	1657	64
Red gurnard	565	7·4	25	172	30
Grey gurnard	199	2·6	32	118	59
Cod	88	1·2	32	56	64
Long rough dab	732	9·6	21	32	4
Norway pout	36	0·5	16	24	67
Lemon sole	321	4·2	23	20	6
Lesser argentine	10	0·1	21	6	60
Horse mackerel	9	0·1	30	5	56
Saithe	37	0·5	39	3	8
Mackerel	4	—	—	3	—
Herring	15	0·2	25	3	20
Witch	90	1·2	25	3	3
Plaice	14	0·2	26	0	0
Megrim	22	0·3	28	0	0
Ling	7	0·1	—	0	0
Skate	3			0	
Angler	3			0	
Dragonet	1			0	
Hake	1			0	

29 cm, respectively, and size-frequency distributions that did not differ from a Normal distribution (Fig. 1).

Fish swallowed

The proportions of each species seen to be swallowed by seabirds differed (Table I). Species for which discards numbered less than 20 have been omitted from statistical comparison, except for flatfish, where all species have been combined into one group. The resulting total number (3776) of discarded fish of the more common discard species seen to be swallowed, as a percentage (50%) of all those discarded, was used to derive expected values (Table II). Whiting, haddock, cod, grey gurnard *Eutrigla gurnardus* and Norway pout were swallowed very much more often than expected by chance, whereas Red gurnard *Aspitrigla cuculus*, Saithe and, in particular, flatfish were swallowed more seldom than expected ($\chi^2_7 = 710$, $P < 0{\cdot}001$). Clearly, scavenging seabirds are selecting certain fish.

Selection of fish species was not identical for all bird species and age classes (Table II). Adult and immature great black-backed gulls *Larus marinus* consumed fish species in different proportions ($\chi^2_5 = 11{\cdot}8$, $P < 0{\cdot}05$). They consumed whiting, haddock, red gurnard, grey gurnard and Norway pout in similar proportions but non-adults swallowed fewer flatfish than did adults and no cod at all. The proportions of each species of fish swallowed by adult gannets was very different from that

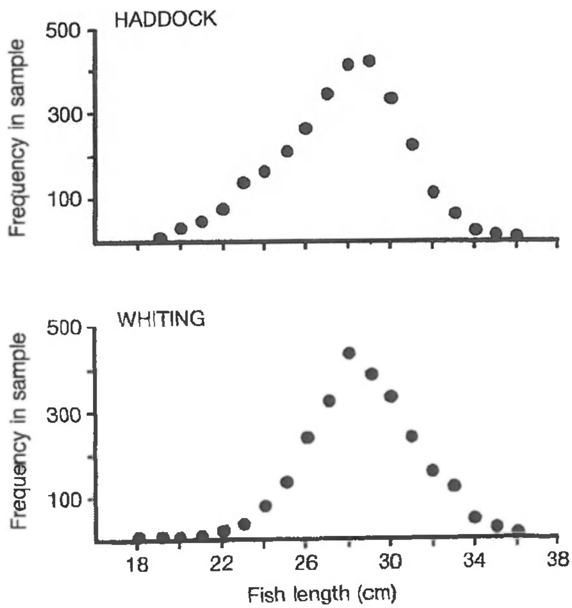

FIG. 1. Distributions of total lengths of samples of haddock and whiting discarded from whitefish trawlers around Shetland in summer 1985.

TABLE II

Numbers of each fish species seen to be swallowed by seabirds following experimental discarding (17 fish of scarce species are omitted). Expected totals are computed assuming that all fish species are swallowed in proportion to availability

Bird species and age class		Whiting	Haddock	Cod	Red gurnard	Grey gurnard	Saithe	Pout	Flatfish	Total	% of total
G. b-b. gull	adult	1025	1126	48	54	45	2	9	46	2355	62·3
G. b-b. gull	3–4 yr	67	96	0	5	4	0	0	0	172	4·6
G. b-b. gull	1–2 yr	110	102	0	6	4	0	1	3	226	6·0
Gannet	adult	129	140	6	107	60	1	0	2	445	11·8
Gannet	1–4 yr	4	3	0	0	0	0	0	0	7	0·2
Herring gull	adult	44	38	2	0	2	0	5	2	93	2·5
Herring gull	1–4 yr	2	11	0	0	0	0	1	0	14	0·4
L. b-b. gull	adult	11	11	0	0	2	0	0	1	25	0·7
L. b-b. gull	1–4 yr	1	6	0	0	0	0	0	0	7	0·2
Great skua	unknown	228	118	0	0	0	0	0	1	347	9·2
Fulmar	unknown	36	40	0	0	1	0	8	0	85	2·3
Total swallowed		1657	1691	56	172	118	3	24	55	3776	
Expected		1295	1429	44	282	100	18	18	590	3776	

TABLE III

Percentages of fish swallowed, dropped or stolen from each bird species. Only fish species listed in Table II are included in this and subsequent tables

Bird species	Age	Swallowed number	(%)	Dropped number	(%)	Stolen from number	(%)	Total handled
G. b-b. gull	adult	2355	89·2	113	4·3	173	6·5	2641
G. b-b. gull	3–4 yr	172	89·1	9	4·7	12	6·2	193
G. b-b. gull	1–2 yr	226	86·2	12	4·6	24	9·2	262
Gannet	all	452	85·8	35	6·6	40	7·6	527
Herring gull	all	107	48·4	56	25·3	58	26·3	221
L. b-b. gull	all	32	38·1	25	29·8	27	32·1	84
Great skua	all	347	63·3	66	12·0	135	24·7	548
Fulmar	all	85	54·5	2	1·3	69	44·2	156
Total numbers		3776		318		538		4632

swallowed by great black-backed gulls ($\chi^2_5=487$, $P<0{\cdot}001$), with great black-backed gulls taking fewer red gurnard and far fewer grey gurnard. Great skuas swallowed more whiting, and less haddock and gurnards, than adult great black-backed gulls ($\chi^2_2=56$, $P<0{\cdot}001$). There was no significant difference between the proportions of fish species swallowed by herring gulls and adult great black-backed gulls. Adult great and lesser black-backed gulls *Larus fuscus* each swallowed whiting, haddock and cod in similar proportions. Fulmars and adult great black-backed gulls each swallowed whiting, haddock and gurnards in similar proportions. Compared with herring gulls, adult gannets swallowed fewer whiting, a similar proportion of haddock and cod and more gurnards ($\chi^2_3=42$, $P<0{\cdot}001$). Gannets also took different fish from great skuas ($\chi^2_3=193$, $P<0{\cdot}001$), swallowing many more gurnards and cod, similar proportions of haddock but less whiting than did the skuas. Herring gulls swallowed more haddock and Norway pout but less whiting than did great skuas ($\chi^2_2=24{\cdot}8$, $P<0{\cdot}001$). In general, the width of flatfish and the bony exterior plating of gurnards, particularly heavy in the red gurnard, resulted in these fish being swallowed less often, and predominantly by the largest seabirds; gannets and great black-backed gulls.

Possibly linked to these differences in selectivity, great black-backed gulls and gannets swallowed over 85% of all fish that they handled, whereas herring gulls, lesser black-backed gulls, great skuas and fulmars swallowed only 38–63% (Table III).

Fish dropped

Many fish that seabirds attempted to swallow were dropped, either because the bird actively rejected the fish once lifted out of the water, or because it made an error of handling while attempting to swallow it in mid-air. In all, 6·1% of all fish handled were seen to be dropped. Herring gulls and lesser black-backed gulls dropped a relatively higher proportion of all fish they handled (Table III) compared to the other bird species.

Furthermore, different species of fish were not dropped in equal proportions by the seabirds, the proportions ranging from 0–21% dropped for each fish species handled. The different fish species were not dropped at random ($\chi^2_6=231$, $P<0{\cdot}001$, Table IV). Very few whiting were dropped and

TABLE IV

Numbers of each species of fish picked up by scavenging seabirds that were dropped

Bird species	Age	Whiting	Haddock	Cod	Red gurnard	Grey gurnard	Pout	Flatfish	Total	% of total
G. b-b. gull	adult	20	24	17	32	1	0	19	113	35·5
G. b-b. gull	3–4 yr	1	5	0	2	0	0	1	9	2·8
G. b-b. gull	1–2 yr	1	3	1	4	1	0	2	12	3·8
Gannet	adult	5	4	0	20	1	0	0	30	9·4
Gannet	1–4 yr	2	0	0	3	0	0	0	5	1·6
Herring gull	adult	16	31	0	2	1	0	0	50	15·7
Herring gull	1–4 yr	0	6	0	0	0	0	0	6	1·9
L. b-b. gull	adult	5	15	0	1	0	0	0	21	6·6
L. b-b. gull	1–4 yr	3	1	0	0	0	0	0	4	1·3
Great skua	all	26	34	0	5	1	0	0	66	20·8
Fulmar	all	2	0	0	0	0	0	0	2	0·6
Total dropped		81	123	18	69	5	0	22	318	
Expected total		140	142	5	18	6	2	5	318	

TABLE V

Observed and expected numbers of fish stolen by and from seabirds, expected numbers being calculated on the assumption that all seabirds are equally likely to steal or be stolen from. P < 0·05 except where shown NS

Seabird species	Age	Expected number	Observed stolen by	Observed stolen from	Chi squared (1 *d.f.*)
G. b-b. gull	adult	254	335	173	51·6
G. b-b. gull	3–4 yr	10	8	12	0·8 NS
G. b-b. gull	1–2 yr	30	36	24	2·4 NS
Gannet	all	49	58	40	3·3 NS
Herring gull	all	31·5	5	58	44·6
L. b-b. gull	all	13·5	0	27	27·0
Great skua	all	114·5	94	135	7·3
Fulmar	all	35·5	2	69	63·2

fewer haddock than expected were dropped. No saithe or Norway pout were dropped but many more cod, red gurnard and flatfish than expected were dropped.

Adult and immature great black-backed gulls dropped similar proportions of whiting, haddock, cod, gurnards and flatfish, but different fish species were more likely to be dropped by different bird species. Compared to adult gannets, adult great black-backed gulls dropped a higher proportion of cod and flatfish, marginally more haddock and less red gurnard than expected ($\chi^2_4 = 20{\cdot}9$, $P < 0{\cdot}001$). Adult great black-backed gulls dropped a smaller proportion of whiting and haddock but a higher proportion of cod, red gurnard and flatfish than expected compared to adult herring gulls ($\chi^2_4 = 44{\cdot}4$, $P < 0{\cdot}001$). Adult gannets dropped very few fish, and most of those dropped were red gurnards.

TABLE VI

Numbers of each fish species stolen by each species from other seabirds behind trawlers. Expected totals for each fish species were calculated using the proportions of each fish species in the total of fish swallowed

Seabird species	Age	Whiting	Haddock	Cod	Gurnard	Pout	Flatfish	Total	% of total
G. b-b. gull	adult	146	161	6	16	0	6	335	62·4
G. b-b. gull	3–4 yr	5	3	0	0	0	0	8	1·5
G. b-b. gull	1–2 yr	15	19	0	1	0	1	36	6·7
Gannet	adult	29	12	1	12	0	0	54	10·1
Gannet	1–4 yr	2	1	0	0	0	0	3	0·6
Herring gull	all	2	3	0	0	0	0	5	0·9
Great skua	all	48	43	0	1	1	1	94	17·5
Fulmar	all	1	1	0	0	0	0	2	0·4
Totals		248	243	7	30	1	8	537	
Expected		236	241	8	41	3	8	537	

TABLE VII

Numbers of each fish species stolen from each seabird behind trawlers at Shetland

Seabird species	Age	Whiting	Haddock	Cod	Gurnard	Pout	Flatfish	Total	%
G. b-b. gull	adult	80	73	5	9	0	6	173	32·2
G. b-b. gull	3–4 yr	4	5	1	2	0	0	12	2·2
G. b-b. gull	1–2 yr	8	15	0	0	0	1	24	4·5
Gannet	adult	17	10	1	11	0	0	39	7·3
Herring gull	all	22	36	0	0	0	0	58	10·8
L. b-b. gull	all	11	14	0	1	1	0	27	5·0
Great skua	all	71	56	0	7	0	1	135	25·1
Fulmar	all	35	34	0	0	0	0	69	12·9

Fish stolen

Birds were seen to fight over fish and to steal fish that other birds were trying to consume. The total number of recorded thefts represented 12% of the number of fish handled by seabirds (Tables III and V), but one fish could be stolen more than once and every bird that stole a fish did not necessarily swallow it. The incidence of kleptoparasitism did not differ significantly between fish species; that is no one fish species was stolen selectively in preference to other species (Table VI).

Some birds stole more fish than they had stolen from them (Tables V, VI and VII). When the total number of fish (of all sizes and all species) stolen by each seabird species was compared to the total number of fish handled, it was also clear that some bird species stole much more frequently than others (Table V). Overall, adult great black-backed gulls and great skuas stole more fish than expected (against the null hypothesis that all birds should stand an equal chance of stealing fish), while immature great black-backed gulls, and gannets, herring gulls, lesser black-backed gulls and fulmars of all ages stole fewer fish than expected ($\chi^2_6 = 57$, $P < 0{\cdot}001$).

TABLE VIII

Mean lengths (cm) of haddock and whiting swallowed by seabirds following experimental discarding from whitefish boats in Shetland in summer 1985. Sample sizes as in Table II

		Fish length swallowed (cm)			
		Haddock		Whiting	
Seabird species	Age	Mean	Standard error	Mean	Standard error
G. b-b. gull	adult	27·9	0·08	28·6	0·08
G. b-b. gull	3–4 yr	27·9	0·29	28·4	0·30
G. b-b. gull	1–2 yr	26·9	0·23	28·5	0·23
Gannet	adult	28·9	0·29	31·0	0·25
Herring gull	adult	25·6	0·39	26·1	0·41
Herring gull	1–4 yr	24·1	0·55	26·5	0·50
L. b-b. gull	adult	25·4	0·72	27·0	1·03
Great skua	all	25·5	0·27	27·4	0·16
Fulmar	all	23·0	0·36	24·1	0·56
All discards		27·6	0·05	28·6	0·05

TABLE IX

Mean lengths (cm) of haddock and whiting dropped by, stolen by, and stolen from, scavenging seabirds. Sample sizes as in Tables V, VI and VII

		Haddock			Whiting		
Seabird species	Age	Dropped	Stolen by	Stolen from	Dropped	Stolen by	Stolen from
G. b-b. gull	adult	29·5	28·1	28·5	30·5	29·1	29·3
G. b-b. gull	1–4 yr	—	27·4	28·9	—	28·1	—
Gannet	adult	—	29·5	28·1	—	32·4	33·1
Herring gull	adult	28·7	—	28·7	29·4	—	28·6
L. b-b. gull	adult	28·7	—	27·9	—	—	30·1
Great skua	all	28·5	26·4	28·3	31·3	28·5	29·9
Fulmar	all	—	—	24·7	—	—	27·3

Great skuas stole the highest proportion of fish, relative to the total number of all fish that they handled, followed by adult great black-backed gulls and then adult gannets. Immature great black-backed gulls stole fewer fish than did the adults. Herring gulls and fulmars stole very few fish and lesser black-backed gulls were not seen to steal at all.

These results were also compared against a null hypothesis that each species and age class of bird should steal as many fish as they had stolen from them. Adult great black-backed gulls stole more fish from other birds than they had stolen from them ($\chi^2_1 = 51{\cdot}6$, $P < 0{\cdot}001$). By contrast, herring gulls ($\chi^2_1 = 44{\cdot}6$, $P < 0{\cdot}001$), lesser black-backed gulls ($\chi^2_1 = 27{\cdot}0$, $P < 0{\cdot}001$), and fulmars ($\chi^2_1 = 63{\cdot}2$, $P < 0{\cdot}001$) lost more fish by kleptoparasitism than they gained. Gannets, great skuas and immature great black-backed gulls lost similar numbers of fish to kleptoparasites as they gained by kleptoparasitism. Over 40% of all fish handled by fulmars were stolen from them.

Sizes of fish swallowed

The mean length of haddock consumed by adult great black-backed gulls (Table VIII) was significantly longer than the mean length of all haddock discarded by fishermen ($t=35$, $P<0.001$), even though the actual difference in fish length was only 0·35 cm. There was no significant difference between the mean lengths of whiting swallowed by adult great black-backed gulls and those discarded. The mean lengths of haddock and whiting swallowed by three and four-year-old great black-backed gulls and of whiting by one and two-year-olds did not differ significantly from the mean lengths of those discarded, but one and two-year-olds swallowed smaller haddock than the mean length discarded ($t=2.7$, $P<0.01$). Adult gannets took larger haddock ($t=4.5$, $P<0.001$) and whiting ($t=41.5$, $P<0.001$) than the average length discarded. The mean lengths of discarded haddock and whiting were significantly greater than the mean lengths swallowed by adult herring gulls ($t=4.9$; $t=5.9$, $P<0.001$), great skuas ($t=7.5$; $t=7.0$, $P<0.001$ and fulmars ($t=12.7$; $t=7.8$, $P<0.001$). Lesser black-backed gulls swallowed haddock that were significantly smaller than the mean length discarded ($t=3.1$, $P<0.01$) but whiting that were of a statistically similar length. However, sample sizes of fish swallowed by lesser black-backed gulls were small.

Sizes of fish dropped

The mean lengths of haddock and whiting that were dropped by seabirds (Table IX) were compared with the mean lengths discarded and swallowed, where sample sizes were greater than ten. The mean lengths of discarded haddock and whiting were less than the mean lengths dropped by adult great black-backed gulls ($t=2.7$, $P<0.01$; $t=2.5$, $P<0.05$) and great skuas ($t=2.18$, $P<0.05$; $t=9.2$, $P<0.001$), and the mean length of discarded haddock was less than that dropped by adult herring gulls ($t=3.2$, $P<0.01$) and adult lesser black-backed gulls ($t=3.27$, $P<0.01$). The mean lengths of dropped haddock and whiting were less than the mean lengths of fish swallowed by great black-backed gulls ($t=2.23$; $t=2.57$, $P<0.05$), adult herring gulls ($t=5.9$; $t=3.5$,

TABLE X

Minimum and maximum lengths of haddock and whiting observed to be swallowed by seabirds behind whitefish trawlers in Shetland in summer 1985

Seabird species	Age	Haddock length (cm)		Whiting length (cm)	
		Minimum	Maximum	Minimum	Maximum
G. b-b. gull	adult	19	38	20	39
G. b-b. gull	3–4 yr	20	33	23	34
G. b-b. gull	1–2 yr	21	32	23	35
Gannet	adult	20	39	24	38
Herring gull	adult	22	31	15	30
Herring gull	3–4 yr	20	27	26	27
Herring gull	1–2 yr	20	25	25	25
L. b-b. gull	adult	22	31	21	33
Great skua	all	18	31	17	35
Fulmar	all	15	30	14	29

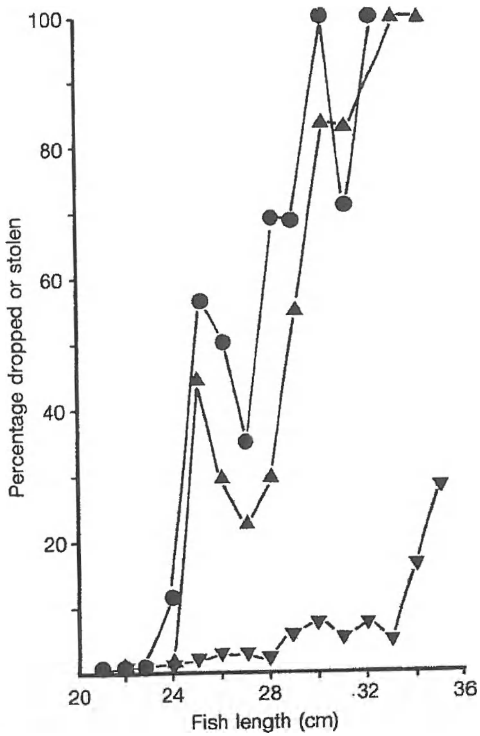

FIG. 2. Percentages of haddock of each length class dropped by or stolen from great skuas (▲), herring gulls (●) and great black-backed gulls (▼).

$P<0.001$), adult lesser black-backed gulls (haddock only, $t=3.7$, $P<0.001$) and great skuas ($t=6.0$; $t=11.8$, $P<0.001$).

The percentage of haddock (Fig. 2) and whiting (Fig. 3) that was dropped by or stolen from great skuas and herring gulls increased with increasing fish length. There was, perhaps, a slight trend for a higher proportion of large fish to be dropped by adult great black-backed gulls but it was not so pronounced as for the two smaller species. Handling haddock was clearly more difficult than handling whiting, as shown by the higher proportion of haddock of each size category that was dropped (Fig. 2 vs. Fig. 3).

Sizes of fish stolen

The mean fish lengths that were stolen from seabirds by other seabirds (Table IX) were compared with the mean lengths of fish swallowed. The mean length of haddock stolen from immature great black-backed gulls was significantly longer than the mean length swallowed by them ($t=2.95$, $P<0.01$) and the same was true for adult herring gulls ($t=9.6$, $P<0.001$), adult lesser black-backed gulls ($t=2.81$, $P<0.01$), great skuas ($t=6.4$, $P<0.001$) and fulmars ($t=2.84$,

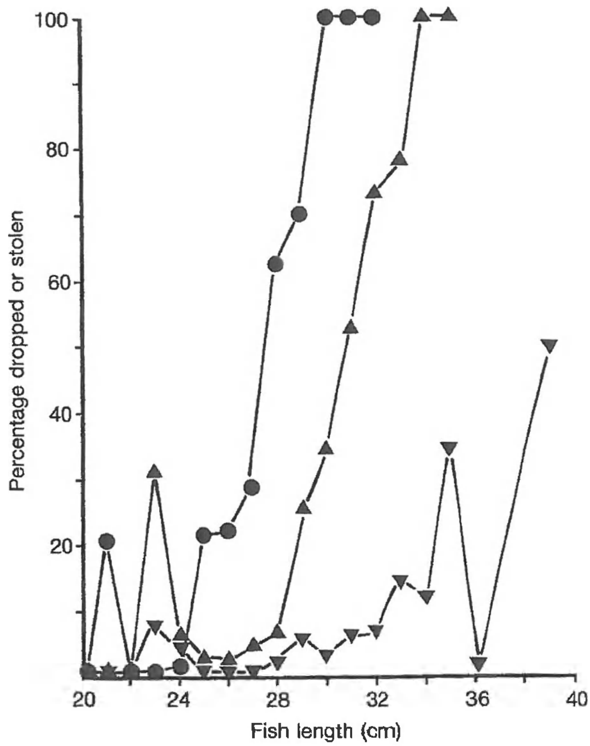

FIG. 3. Percentages of whiting of each length class dropped by or stolen from great skuas (▲), herring gulls (●) and great black-backed gulls (▼).

$P<0\cdot01$). The mean length of whiting stolen from birds was longer than the mean length swallowed by each species for adult great black-backed gulls ($t=2\cdot31$, $P<0\cdot05$), adult gannets ($t=2\cdot39$, $P<0\cdot05$), adult herring gulls ($t=3\cdot88$, $P<0\cdot001$), adult lesser black-backed gulls ($t=2\cdot61$, $P<0\cdot01$), great skuas ($t=9\cdot0$, $P<0\cdot001$) and fulmars ($t=7\cdot3$, $P<0\cdot001$).

The mean lengths of haddock stolen by adult and immature great black-backed gulls, adult gannets and great skuas did not differ significantly from the mean lengths swallowed by each species (Table IX), nor did the mean length stolen by immature great black-backed gulls. However, adult great black-backed gulls stole whiting that were longer than the mean length that they swallowed ($t=2\cdot40$, $P<0\cdot05$), as did adult gannets ($t=2\cdot10$, $P<0\cdot05$). Great skuas also stole whiting that were longer than the mean length they swallowed ($t=3\cdot22$, $P<0\cdot01$).

The mean discard lengths of haddock and whiting stolen from adult great black-backed gulls did not differ significantly from those stolen by them. The same was true for adult gannets and for haddock stolen by and from immature great black-backed gulls. However, the mean lengths of haddock and whiting stolen from great skuas were longer than the mean lengths stolen by great skuas ($t=2\cdot97$, $P<0\cdot01$; $t=3\cdot20$, $P<0\cdot002$).

Maximum sizes of discards consumed by seabirds

Some indication of the maximum length of fish that birds could handle was gathered by watching birds go towards fish and then leave them, or else try to pick up fish that were too large for them to manage to swallow, and also by examining the maximum lengths of fish seen to be swallowed (Table X). In general, larger seabird species were able to swallow larger fish, and often ignored the smallest discards. Herring gulls and fulmars were unable to swallow a large proportion of the fish discarded, while gannets and great black-backed gulls could swallow all but the very largest discards.

Discussion

Fish species preferences

Clearly scavenging seabirds select discards according to species and size. Few flatfish were swallowed or dropped, and so by implication, most discarded flatfish were left to sink by the seabirds. Nearly 30% of all flatfish picked up were dropped again, whereas less than 5% of all whiting handled were dropped. Red gurnards, although generally smaller than the average discard, also proved to be less popular than whiting, haddock or Norway pout, presumably because red gurnards have a hard external covering and so are more difficult to swallow than are gadoids of a similar size. However, the percentage of grey gurnards swallowed was the same as for haddock, so clearly the seabirds find the two gurnard species very different to handle.

Differences in fish selection by different seabirds show that adult great black-backed gulls had less difficulty in coping with larger fish and with difficult species like flatfish, whereas immatures were less successful in swallowing these. Similarly, the smaller seabirds tended to be more restricted in the range of discards they could swallow. Great skuas in particular, selected small whiting by preference. Whiting are narrower at the head than are haddock (Hudson, 1986), and so are easier to swallow. Larger seabirds, particularly gannets, showed less selectivity, taking red gurnards and larger fish that the smaller seabirds avoided or were unable to handle successfully.

Feeding efficiency and kleptoparasitism

That 12% of fish handled by seabirds were stolen from them is evidence of the competitive nature of feeding by scavenging seabirds at trawlers. Flocks may consist of several hundred seabirds attempting to obtain fish that are being discarded at a steady trickle.

Although all age classes of great black-backed gulls stole more fish than they had stolen from them, adults stole proportionately very many more, and had fewer fish taken from them. Adults took longer fish than non-adults and they also handled the fish more quickly (Hudson, 1986). Increased adult efficiency and success has also been recorded for the herring gull around *Nephrops* trawlers in the Clyde, where adults dropped fewer fish, were more selective in the size of fish they chose and overall they obtained more fish then did immatures (Furness *et al.*, In press).

Juvenile and immature birds are usually less efficient foragers than adults (e.g. Dunn, 1972; Cook, 1978) and efficiency at feeding improves slowly with age, as shown for herring gulls feeding at refuse tips (Greig, Coulson & Monaghan, 1983). In Mexico, adult laughing gulls (*Larus atricilla*) chose juvenile brown pelicans (*Pelecanus occidentalis*) in preference to adults as their victims for kleptoparasitic attacks, even though adult brown pelicans were more successful in their foraging attempts than juveniles. Juveniles were less efficient at evading kleptoparasitic attacks by the gulls, thereby increasing the food available for the laughing gulls (Carroll & Cramer, 1985). At rubbish dumps in New Jersey and Mexico, adult herring and ring-billed gulls (*Larus delawarensis*) engaged in kleptoparasitism more often than young gulls and also they were chased less often than were young gulls, although there were no differences in kleptoparasitic success rates (Burger & Gochfeld, 1981). In that study, the larger great black-backed gulls were seldom victims of kleptoparasitic attacks. When laughing gulls in Mexico were supplied with lumps of chopped liver, adults were more successful than non-adults; the younger gulls were unable to obtain and keep the larger pieces. Improvement occurred with age and experience.

Kleptoparasitism is particularly common amongst certain families of seabirds, and skuas are often considered to be 'specialist kleptoparasites', whereas gulls are considered to be 'opportunists' (e.g. Brockmann & Barnard, 1979; Furness, 1987). During the present study, great skuas showed the highest frequency of kleptoparasitism, but they were less successful than great black-backed gulls because they lost more fish to other kleptoparasites than they actually gained. This may have been due to the fact that the fish were rather long for great skuas to handle efficiently (Hudson, 1986) rather than the fact that they have less well-developed kleptoparasitic skills than the larger gulls. Their predilection to steal food from other birds may have been disadvantageous in this foraging situation, since much energy is expended in kleptoparasitic chases and rewards for great skuas were not good. Many of the fish being discarded were too large for the skuas to swallow quickly and therefore they carried the fish for longer than did the great black-backed gulls. The mean length of discards stolen from great skuas was greater than the mean length stolen by them, which suggests that those fish that were stolen from them were too large for them to handle efficiently. Conspicuous prey probably increases the likelihood of kleptoparasitism (Brockmann & Barnard, 1979; but see Furness, 1987); either the fish size or the length of time taken to handle the fish could be the key in determining conspicuousness of prey. In the Minas Basin in Nova Scotia, fish that were large and took a long time to handle were the only ones to be stolen from great blue herons (*Ardea herodias*) by gulls. Small fish could be swallowed quickly, thus minimizing the time in which another bird could steal the fish (Quinney, Miller & Quinney, 1981).

Brockmann & Barnard (1979) report that kleptoparasitism is especially common amongst mixed flocks of birds and such a situation was observed behind the whitefish trawlers in the present study. Great skuas do not restrict their kleptoparasitic activities to fish being discarded at sea but steal prey from many seabird species at their breeding colonies (e.g. Andersson, 1976; Furness, 1978). Thus kleptoparasitism by great skuas at sea is not purely an adaptation to prevailing circumstances but is part of the feeding behaviour of the great skua during the breeding season. Kleptoparasitism has been recorded for herring and lesser black-backed gulls (Verbeek, 1977) but was not common behind whitefish trawlers in Shetland. It is probable that the relatively large size of the discards carried by seabirds meant that herring gulls and lesser black-backed gulls would have generally been unable to steal them from the larger seabirds.

Implications for the scavenging seabird guild in Shetland

Between 59% and 67% of all whiting, haddock, cod and Norway pout discarded was seen to be swallowed by scavenging seabirds (Table I). Almost certainly most of those for which the ultimate fate was not seen were also swallowed, since the few fish seen to sink without being lifted by seabirds were all flatfish or gurnards. Thus the demand for discards around Shetland trawlers equals or exceeds the availability of suitable fish. Competition between scavenging seabirds is thus inevitable, and is manifest in the frequent stealing of fish and by the tendency for gannets and great skuas to displace gulls from the area where most discards land behind the trawler (Hudson, 1986). The fact that gannets and great black-backed gulls can swallow a wider variety of fish species and a wider range of fish sizes more easily undoubtedly gives these species an advantage when exploiting discards around Shetland. The rather unexpected finding that great skuas have more fish stolen from them than they manage to steal in this situation highlights the disadvantages that the smaller scavenging seabirds have in attempting to compete for the large discards thrown overboard by Shetland boats.

This situation differs markedly from that found in some other areas. In the Clyde Sea for example, *Nephrops* trawlers discard fish that are generally less than 20 cm in length, and so these fish are easily swallowed by herring gulls and lesser black-backed gulls, which are abundant around fishing boats in the Clyde (Furness *et al.*, In press) but are greatly outnumbered by great black-backed gulls at Shetland boats.

Although scavenging seabirds make extensive use of discards around Shetland, only the larger species can exploit this food supply efficiently. The fulmar in particular obtains very few discards; only 2% of discards seen to be swallowed were taken by fulmars and yet fulmars obtain almost all of the offal because they greatly outnumber all other species and can drive competitors away from offal (Hudson, 1986; Furness *et al.*, In press). The fulmar's inability to swallow large discards appears to be due to anatomical constraints. This study has shown that discards form an important source of food for gannets, great black-backed gulls and great skuas around Shetland in summer. The large size of fish discarded, together with competition from larger seabirds, precludes kittiwakes, fulmars and herring gulls from exploiting discards to a large extent, during the summer months at least. Great skuas have to select only smaller fish of easily-swallowed species, and are robbed of many of these.

In January 1987, the legal minimum net-mesh size to be used by whitefish trawlers in the North Sea was increased by 5 mm, to 85 mm. Further increases are likely, as part of an attempt to utilize stocks better and to reduce wasteful discarding and growth overfishing. This change may have important repercussions for scavenging seabirds, since the mean size of discards will increase, and the quantity of fish discarded should decrease. Most severely affected by such changes would be the smaller scavenging species, and the great skua in particular may be forced to turn to alternative feeding methods, such as predation of auks and kittiwakes. The study reported here provides a valuable quantitative baseline against which future effects of increased net-mesh size may be compared.

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