

Distribution of ship-following seabirds and their utilization of discards in the North Sea in summer

Stefan Garthe^{1,2}, Ommo Hüppop¹

¹Institut für Vogelforschung 'Vogelwarte Helgoland', PO Box 1220, D-27484 Helgoland, Germany

²Institut für Meereskunde, Abt. Meereszoologie, Düsternbrooker Weg 20, D-24105 Kiel, Germany

ABSTRACT: Prey availability is one of the factors determining the distribution of seabirds at sea. Northern fulmars *Fulmarus glacialis* and black-legged kittiwakes *Rissa tridactyla* were the most regular and frequent ship-followers across the central and northern North Sea during 2 surveys with a fishery research vessel in May–June and July–August 1992. Sixteen other species occurred less often and/or in lower numbers. Birds consumed 84 % of experimentally discarded roundfish and 8 % of discarded flatfish. On average, northern gannets *Morus bassarius* took the largest individuals of most fish species, black-legged kittiwakes the smallest. The average size choices of herring gulls *Larus argentatus*, lesser black-backed gulls *Larus fuscus* and northern fulmars lay between these 2 extremes. The choice of fish lengths by birds varied with different fish species. Northern gannet was the most successful species in consuming discards. Northern fulmars success rates decreased with the presence of larger ship-followers but were never high. Black-headed gull *Larus ridibundus* and common gull *Larus canus* were less successful than the more frequent, typical ship-following species.

KEY WORDS: Seabirds • North Sea • Fisheries • Discards • Feeding ecology

INTRODUCTION

The distribution of seabirds at sea is patchy at various scales. The processes responsible include hydrographical mechanisms, active and passive movements of prey and the social behaviour of birds (Lunt 1988). These factors are of variable relative importance in different parts of the world's oceans. Although the location of breeding sites influences seabird feeding distribution, fisheries also have a strong influence at a smaller scale on the distribution of seabirds at sea, as seen in the North Sea (Tasker et al. 1987), the Benguela Current (Ryan & Moloney 1988) and the Eastern Pacific (Wahl & Heinemann 1979).

Studies near the Shetland Islands and in the Clyde area west of Scotland, UK, gave first information on the use of fishery wastes by seabirds (Furness et al. 1988). A first study covering the whole North Sea in winter 1993 confirms the assumption that seabirds benefit enormously from this type of food resource (Campbellsen et al. 1993). Populations of most seabird and some coastal bird species in the North Sea have grown con-

siderably in the last few decades, probably as a result of improved food conditions provided by whaling and fisheries (Vauk et al. 1989, Dunnet et al. 1990, Lloyd et al. 1991). Presently about 1.2 million seabirds, feeding at least partially on discards and offal, breed around the North Sea (Furness 1992).

Interspecific competition evoked by the supply of discards and offal has already led to changes in the avifauna of seabirds and coastal birds (Furness et al. 1992, Noordhuis & Spaans 1992). Further changes in catch composition due to larger mesh sizes will probably cause higher competition for discards and offal. Decreasing populations of the weaker scavenging species are to be expected. Therefore it is essential to obtain detailed data about the utilization of discards by scavenging seabirds. This includes not only the choice of different fish species and their lengths but also the rates at which discards are taken by birds. To evaluate interspecific competition and its possible consequences, it is also important to know the distribution and numbers of ship-followers.

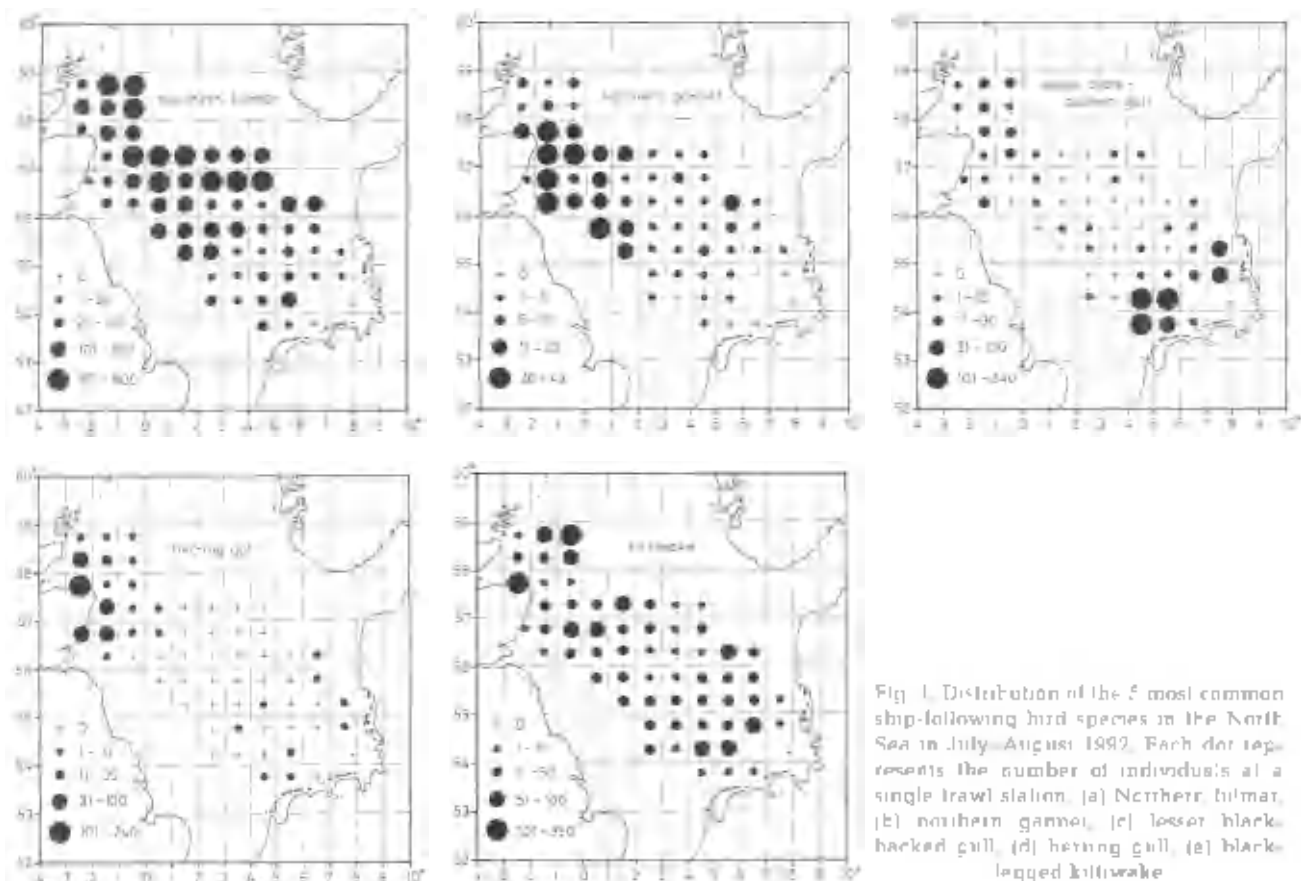


Fig. 1. Distribution of the 5 most common ship-following bird species in the North Sea in July–August 1992. Each dot represents the number of individuals at a single trawl station. (a) Northern fulmar, (b) northern gannet, (c) lesser black-backed gull, (d) herring gull, (e) black-legged kittiwake

Northern gannets were seen in higher numbers in the western part of the North Sea than in the other areas (Fig. 1b). They were numerous only near the colony at Bass Rock in the Firth of Forth, Scotland, but they were present in low numbers at nearly all trawl stations, except a few in the German Bight.

Lesser black-backed gulls occurred in considerable concentrations close to the Dutch and German coast, and in lower numbers near the Scottish coast (Fig. 1c). The highest numbers of herring gulls were found close to the Scottish coast, with low numbers in the south-eastern part of the study area (Fig. 1d). Both herring gull and lesser black-backed gull were hardly recorded in central parts of the North Sea. Their maps resemble those presented in Tasker et al. (1987). Despite a much lower breeding population in the southeastern part of the study area (Furness 1992), the numbers of lesser black-backed gulls there were many times higher than those of herring gulls, presumably because lesser black-backed gulls may utilize fishery wastes near the Wadden Sea to a higher degree than herring gulls (see Noordhuis & Spaans 1992).

Black-legged kittiwakes were more evenly distributed. Slightly higher numbers were found in the southeastern and northwestern parts of the North Sea

(Fig. 1e). Even in the central and eastern part of the study area, black-legged kittiwakes were found in surprisingly high numbers, which stands in contrast to the maps in Tasker et al. (1987).

Choice of fish species and length

Nearly all length classes of offered fish were utilized by ship-following seabirds due to the broad spectrum of bird species (Fig. 2). In all fish species (see Table 2 for scientific names) we notice much overlap in their utilization by bird species. However, average length choices of the fish species taken varied among the most common ship-following bird species, northern fulmar, northern gannet, lesser black-backed gull, herring gull and black-legged kittiwake. Significant differences (Kruskal-Wallis H test) between these bird species occurred in the choice of lengths of whiting ($\chi^2 = 210.9$, $p < 0.0001$, $n = 864$), poor cod ($\chi^2 = 131.6$, $p < 0.0001$, $n = 259$), Norway pout ($\chi^2 = 48.7$, $p < 0.0001$, $n = 1318$), haddock ($\chi^2 = 183.5$, $p < 0.0001$, $n = 497$), herring ($\chi^2 = 266.1$, $p < 0.0001$, $n = 1046$), sprat ($\chi^2 = 36.9$, $p < 0.0001$, $n = 240$) and grey gurnard ($\chi^2 = 9.72$, $p < 0.05$, $n = 66$). No differences were found for sand

eels ($\chi^2 = 3.38$, not significant, $n = 173$). Northern gannets took the largest mean lengths of all fish species except poor cod, black-legged kittiwakes the smallest. Common gulls and black-headed gulls, which were not present as often as other species, behaved much like black-legged kittiwakes in their length choices. In most cases, northern fulmars, great skuas *Caitharacta skua*, lesser black-backed gulls, herring gulls and great black-backed gulls *Larus marinus* were intermediate between northern gannets and black-legged

kittiwakes in their choices of fish lengths. Great black-backed gulls and great skuas tended towards greater lengths, whereas herring gulls and lesser black-backed gulls were inclined to select intermediate lengths. Some of the variability in the mean lengths of fish chosen by different ship-following bird species can be explained by their body measures (Table 1). Body lengths of birds correlated with length choice in 4 out of 6 fish species, body mass and bill length on 2 occasions each.

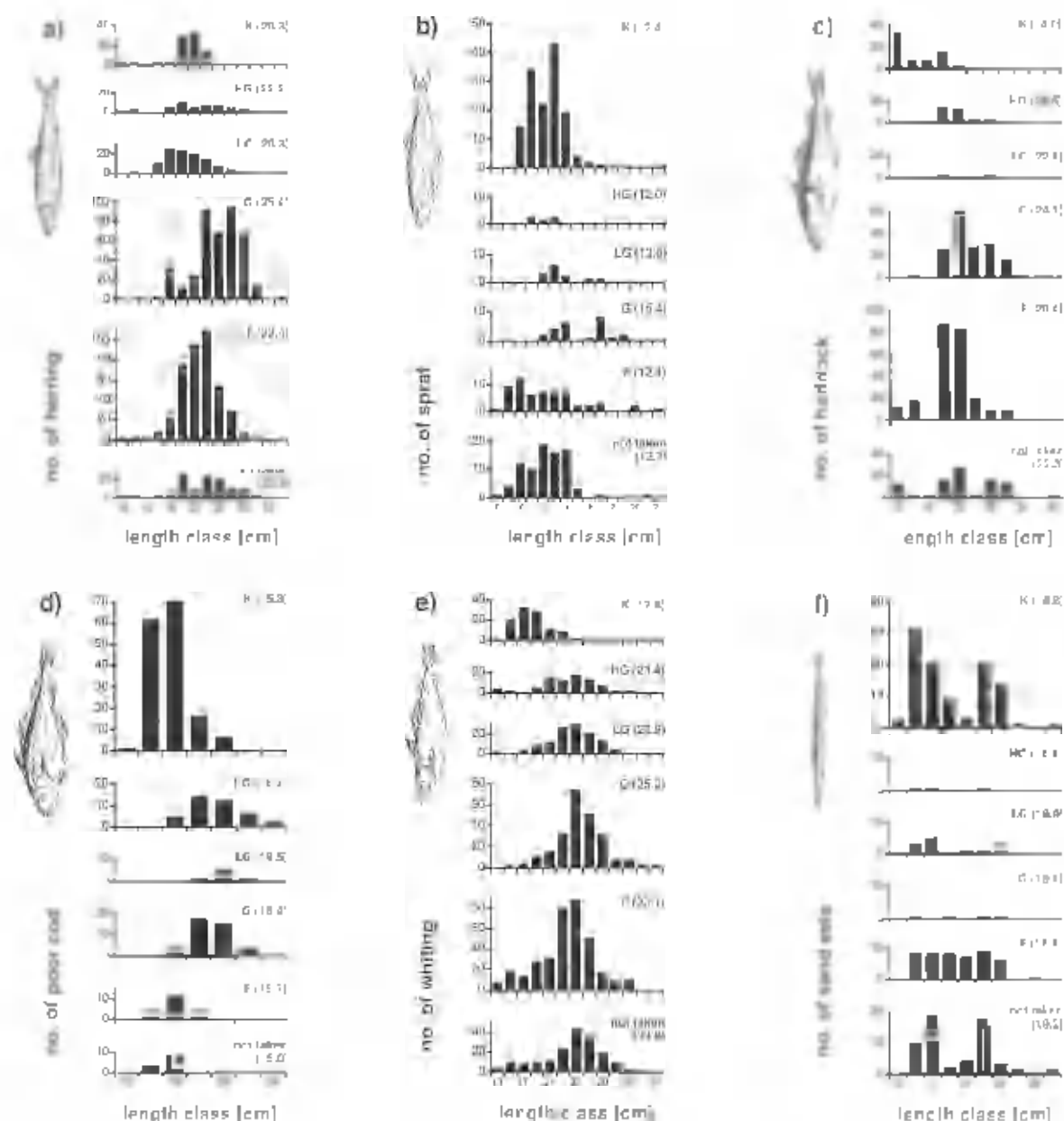


Table 1. Body masses, body lengths (after Rezzel 1985) and bill lengths (after Cramp & Simmons 1977, 1983) of the most numerous bird species and their correlations with average fish lengths. Significant correlations ($p < 0.05$) are underlined

Species	Body mass (g)	Body length (mm)	Bill length (mm)
Black-legged kittiwake	371	490	34.0
Northern fulmar	781	475	39.3
Lesser black-backed gull	792	595	51.9
Herring gull	1061	610	54.9
Northern gannet	3015	935	98.4
Coefficient of correlation			
$r_{\text{total fish}}$	0.360	0.274	0.273
r_{gannet}	0.875	0.866	<u>0.886</u>
r_{fulmar}	0.927	0.840	0.857
r_{gull}	0.666	0.794	0.721
r_{gull}	0.409	0.671	0.557
r_{gull}	0.662	0.720	0.697

Length ranges of fish species taken also differed considerably between the different bird species (Table 2). Northern gannets and northern fulmars took the longest individuals of most fish species. Northern fulmars showed a highly variable utilization of offered fish lengths due to their pecking of offal out of the fish bodies, especially from large specimens of which the remains sank later etc. In this manner they achieve an expanded length spectrum. Common gulls, black-headed gulls and black-legged kittiwakes took predominantly smaller fish, i.e. the maximum lengths of the fish species chosen often lay distinctly below those selected by larger bird species.

Black-legged kittiwakes and the other 4 bird species had a clear size separation for whiting, porcod and haddock (Fig. 2). In contrast, length choices for sand eels, sprat and herring overlapped considerably between these bird groups. Similarly, a clear separation between northern gannets and northern fulmars (large gulls occurred for haddock and herring, but not for sand eels and only slightly for whiting and porcod). In most cases, northern fulmars and large gulls overlapped to a great extent in their length choices of offered fish.

Different natural lengths of fish may explain some of these results. It is either not possible, especially for smaller bird species, to swallow larger fish such as cod. On the other hand, all common ship-following seabirds can manage sprats at any time. Realistic comparisons may only be applicable if either parameters of fish body dimensions are considered. The lack of significance in the comparison of length choices for sand eels and the largest mean of taken sand eels by the smallest bird species, the black-legged kittiwake, showed that length is not the only

parameter of interest for birds, as already shown by Swennen & Duiven (1977) for 3 species of alcids.

Success index

In both the May-June and July-August surveys, northern gannet was the species most successful at getting fish (Table 3). Herring gull, black-legged kittiwake, pomarine skua *Stercorarius pomarinus*, lesser black-backed gull, great black-backed gull and northern fulmar followed within a close range. Even lower success indices were found for great skua, common gull, black-headed gull and finally common tern *Sterna hirundo* and arctic tern *Sterna paradisaea*.

Northern gannets were most successful in taking offered fish. The success of northern fulmars depended strongly on the quantitative composition of other ship-followers but was never very high. They succeeded least during trawls where all bird species were present. Absence of species with food piracy behaviour, such as great skua, northern gannet and great black-backed gull, leads to higher success indices. Black-headed gull and common gull were less successful than the other, more typical ship-following species. However, the extra food provided by fishing vessels could help them satisfy their energy demands during moult.

Analyses of those hauls during which all the bird species considered were present gave more detailed results: northern gannet and black-legged kittiwake showed a relatively constant success rate, whereas northern fulmar was more successful in the absence of larger species such as northern gannet, great skua and great black-backed gull. Success indices of lesser black-backed gull and herring gull were highly variable, showing no clear tendencies.

How accurate is this mean success index? Since we have no information about the length of time birds stay behind vessels, we do not know how many individuals per species actually attend a trawl and the conservative processing. Enksted et al. (1988) determined an average of 480 to 591 min for black-legged kittiwakes following a ship in the Barents Sea in August 1986. The vessel trawled regularly every 20 to 30 n miles. Between the trawl stations the birds rested on the ship. With few exceptions this observation could not be confirmed on either of the 'Walther Heiwig' journeys. Thus, a shorter following time seemed probable. Hudson & Furness (1989) mention that the average

Table 2. Numbers of fish offered to and eaten by birds, and length ranges (in cm) of fish not taken and eaten by birds in the North Sea

Species	No. of fish offered	Fish offered (%)	Length									
			Not taken	Not eaten	Not taken	Crustaceans	Parkish gull	Common gull	FRR gull	Herring gull	GRR eul.	Black-billed gull
Total number	11 991	82	2485	4451	2251	57	20	54	94F	804	148	2965
Norway pout <i>Trisopterus esmarki</i>	1279	66	12-20.5	10-22	12-20	15-16	15-16	14-18	12-20.5	15-20	14-20	11-21.5
Pothead <i>Trisopterus minutus</i>	279	98	13-16	13.5-19.5	16-21	-	-	-	18-21	15.5-24	-	12-20
Herring <i>Clupea harengus</i>	2419	90	10-31	10-31	12-36	23-31	15-17	12-20	11-26	11-31	16-33	9-24
Lesser argentine <i>Argentina sphyraena</i>	55	84	15-27	15-23	17	-	-	-	12-20	-	17-19	16-19
Whiting <i>Merlangius merlangus</i>	1629	83	7-34	11-43	15-37	18-31	11	19-21	13-31	13-36	17-32	13-27
Haddock <i>Melanogrammus aeglefinus</i>	1458	80	10-40.5	10-38	12-39.5	29	17	12-13	11-28	11-31	12-29	10-21
Sprat <i>Sprattus sprattus</i>	867	77	8-21	7.5-25	8-15	-	10-14	11-12	11-17	11-12	-	9-17
Filchard <i>Sardinia pilchardus</i>	70	75	25-28	-	-	-	-	-	27-28	25-29	-	-
Sand eels <i>Ammodytes</i> sp. <i>Hyperoplus</i> sp.	649	72	14-31	14-28	14-25	-	16	-	14-25	14-25	-	13-31
Cod <i>Gadus morhua</i>	185	70	14.5-47	8-57	21-23	-	7	10	14-22	10.5-29	29	10-18
Grey gull <i>Guillemus guillemus</i>	226	55	12-35	12-24	16-33	-	13	-	13-24	14-27	18-28	10
Mackerel <i>Scomber scombrus</i>	161	52	21-35	24-25	25-36.5	-	-	-	21-29	24-28	-	-
Reckings <i>Rhinonemus ambrus</i> etc.	74	42	12-28	18	-	-	-	-	15-24	-	-	12-21
Dreggøet <i>Callionymus lyra</i>	19	37	16-24	17	20-21	-	12	-	16-22	24	-	-
Scad <i>Trachurus trachurus</i>	110	36	21-33	28-30	25-33	-	-	-	21-30	22-30	-	12
Lemon sole <i>Microstomus kitt</i>	19	21	18-35	-	22	-	-	-	-	-	18-25	-
Long rough dab <i>Flippoglossus platessoides</i>	59	8	10-25	-	16.5	-	-	-	19-20	-	-	-
Dab <i>Limanda limanda</i>	377	7	12-26	13-19	14-22	-	-	-	11-24	17-19	-	-
Caligone <i>Caligone caligone</i>	165	18	-	-	-	-	-	-	-	-	-	-
Other fish	1	0	-	-	-	-	-	-	-	-	-	-

number of northern gannets received at any particular station near a hawley is merely an indication of the total number of hawleys appear to have a high turnover rate in following ships.

Proportion of discarded fish consumed

The ship-following bird species showed a substantial utilization of discarded fish species and lengths. The proportion of discards taken by birds varied between 7 and 98%, depending on the fish species (Table 2). Gull and Crustaceans were taken at highest rates, almost all Norway pout and pothead were eaten, with herring, lesser argentine, whiting and haddock being next. The slightly lower rate for cod may be explained by its greater mean length compared to haddock and whiting. Survival of the small mesh size, some species such as pothead and especially Norway pout, were often too small to be caught in commercial nets. Also larger individuals of herring and cod (e.g. backcod, whiting, cod) are usually discarded and not separated from commercial vessels. Flounder were hardly taken because they are difficult to handle (Hudson 1989, petersen 1991). Since all fish discarded were dead, the possibility of a higher survival rate of flounder at the carrying (Bergheim et al. 1992) can be ruled out. On the whole 64% of all fish catch and 8% of all flounder offered were taken by birds. Despite the quite different conditions on a vessel, our figures come close to the percentages taken by birds following Scottish herring trawlers (median of 58 and 5% respectively; Hudson & Furness 1988, Furness 1990) or hawleys in the German Wadden Sea (68 to 94% for small *Osmerus* specimens and 73 to 82% for whiting; Bergheim & Posner 1992).

This study helps to develop a quantitative approach to the interactions of fishery and seabirds. The ultimate question (are rough fishery waste do seabirds actually consume?) could not be answered, since especially the feeding rate (Table 2) is assumed to be lower in commercial fisheries (Carling 1991, large quantities of all once (Camp-huisen et al. 1993) compared to our study of scolding single fish. Also, the type and amount of discards are different from com-

Table 1. Success indices of the most common ship-following bird species in the North Sea 1992. Average values for all hauls with presence of the species are shown in the first 3 columns, the next 2 columns give the number of hauls in which the species occurred, the final 2 columns present these as percentages of total hauls. May-June, n = 56 hauls; July-August, n = 51 hauls; —, not present

	May-June	July-August	Both journeys combined	No. of hauls with species present			
				May-June (n)	July-August (n)	May-June (%)	July-August (%)
Northern gannet	80	71	76	48	47	82	84
Herring gull	34	45	38	78	28	68	55
Black-legged Kittiwake	34	40	37	56	40	100	96
Femoral skua	—	36	36	0	7	0	4
Lesser black-backed gull	33	38	35	40	36	71	75
Great black-backed gull	40	28	31	6	18	11	37
Northern fulmar	37	25	31	56	51	100	100
Great skua	30	22	24	3	21	5	41
Common gull	0	24	23	1	26	2	57
Black-headed gull	0	20	19	0	16	5	35
Common tern / Arctic skua	—	4	4	0	11	0	22

mercial fisheries. However, 2 quite tangible examples illustrate the importance of discard use: on 15 July 1992, a ca 4 yr old northern gannet was observed to swallow 5 mackerel (25 cm, 3 × 26 cm, 28 cm) and a whiting (22 cm), which were experimentally discarded, in less than 10 min. Using length-mass relationships in Daan (1975) and energetic values provided by Sidwell (1981) for mackerel muscle and Hislop et al. (1991) for whiting, the total energy consumed was 5675 kJ. Assuming an utilization efficiency of 80% (Wiens 1984, Castro et al. 1989), 4700 kJ remained for the northern gannet. Birt-Friesen et al. (1989) determined a field metabolic rate (FMR) of 4865 kJ d⁻¹ for feeding adults in Newfoundland, Canada. This implies that the northern gannet observed in the southern North Sea met its energy demands for more than a day as a nonbreeding individual with less energy costs than a breeding adult within those 10 min.

Another energy consideration could be formulated as follows: how many fish does a herring gull need each day? Hüppop (1987) estimated that nonbreeding individuals require 940 kJ d⁻¹. Thus, herring gulls can meet their energy demands for 1 day by eating a cod of 71 cm or 2 plaice of 25 cm estimated by length-mass relationships in Daan (1975) and by energetic values in Sidwell (1981). These energetic aspects show the enormous potential of fishery wastes in providing a supplementary food source to seabirds. Further studies, e.g. on the turnover rate of species and their age groups at the vessels, would describe the situation of competition more precisely.

Acknowledgements. We thank the Bundesforschungsanstalt für Fischerei (Federal Research Board for Fisheries) in Hamburg for the opportunity to take part in the journeys of the fishery research vessel 'Walther Herwig'. The cruise leaders (Siegfried Ehrlich and Holger Dornheim) and Captain Hinners

and his crew let us work on board the vessel. The visiting help of Stefan Probst, Fritz Clausen and Kirsten Jansen and seavard look and engine hires was essential for the project. Thanks also to the 'Freunde und Förderer der Inselkibber der Vogels' 'Heinrich & V.' for financial support, Karin Mathias for checking our English, Robert W. Furness, Frans Beintjes and Peter Menck for improvements on a first draft of this text, Ingrid Hüppop for drawing the maps, and to Kerstin Kober for the vignettes of the fishes.

LITERATURE CITED

- Anonymous (1990). Report of the International North Sea, Skagerrak, and Kattegat Bottom Trawl Survey working group ICES-CM 1990/H.3.
- Berghahn, R., Römer, H.-H. (1992). A method to quantify feeding of seabirds on discard from the shrimp fishery in the North Sea. *Neth. J. Sea Res.* 28: 347-350.
- Berghahn, R., Wallemann, M., Rijnsdorp, A. D. (1992). Mortality of fish from the by-catch of shrimp vessels in the North Sea. *J. appl. Ichthyol.* 8: 293-306.
- Bezzel, E. (1985). Kompendium der Vogel Mitteleuropas. Nonpasseriformes — Nichtsingvögel. Aula, Wiesbaden.
- Birt-Friesen, V. L., Monlevent, W. A., Cairns, D. K., Marko, S. A. (1989). Activity specific metabolic rates of free-living Northern Gannets and other seabirds. *Ecology* 70: 357-367.
- Camphuysen, C. J., Enser, K., Furness, R. W., Garthe, S., Hüppop, O., Leaper, G., Olthoff, H., Tasker, M. L. (1993). Seabirds feeding on discards in winter in the North Sea. EC DG XIV research contract 92/2505. NIOZ rapport 1993.8. Netherlands Institute for Sea Research, Texel.
- Castro, G., Sioyan, N., Myers, J. P. (1989). Assimilation efficiency in birds: a function of taxon or food type? *Comp. Biochem. Physiol.* 92A: 271-278.
- Cramp, S., Simmons, K. E. L. (eds.) (1977). Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic, Vol. 1. Ostrich to ducks. Oxford Univ. Press, Oxford.
- Cramp, S., Simmons, K. E. L. (eds.) (1983). Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic, Vol. 2. Waders to gulls. Oxford Univ. Press, Oxford.

- Daan N. (1975). Consumption and production in the North Sea cod *Gadus morhua*: an assessment of the ecological status of the stock. *Neth. J. Sea Res.* 9: 24–55.
- Dunnet, G. M., Furness, R. W., Tasker, M. L., Becker, P. H. (1990). Seabird ecology in the North Sea. *Neth. J. Sea Res.* 26: 387–425.
- Dunnet, G. M., Gilliam, J. C. (1978). Survival and longevity in the fulmar *Fulmarus glacialis*. *Ibis* 120: 124–125.
- Erikstad, K. F., Rustnes, J. O., Jacobsen, O. (1988). Duration of ship-following by Killiwakes *Rissa tridactyla* in the Barents Sea. *Polar Res.* 6: 191–194.
- Furness, R. W. (1987). Implications of changes in net mesh size, fishing effort and minimum landing size regulations in the North Sea for seabird populations. JNCC Rep. No. 177. Joint Nature Conservation Committee, Offshore Animals Branch, Aberdeen.
- Furness, R. W., Ensor, K., Hudson, A. V. (1992). The use of fishery waste by gull populations around the British Isles. *Ardea* 80: 105–117.
- Furness, R. W., Hudson, A. V., Ensor, K. (1998). Interactions between scavenging seabirds and commercial fisheries around the British Isles. In: Burger, L. (ed.) *Seabirds & other marine vertebrates: Competition, predation, and other interactions*. Columbia Univ. Press, New York, p. 240–268.
- Furness, R. W., Todd, C. M. (1984). Diets and feeding of Fulmars *Fulmarus glacialis* during the breeding season: a comparison between St Kilda and Shetland colonies. *Ibis* 126: 379–387.
- Hislop, J. R. G., Hains, M. P., Smith, J. G. M. (1991). Variation in the caloric value and total energy content of the lesser sand eel (*Ammodytes marinus*) and other fish preyed on by seabirds. *J. Zool., Lond.* 224: 501–517.
- Horton, N., Brough, T., Fletcher, M. R., Rochard, J. R. A., Stanley, P. I. (1984). The winter distribution of Invergla Black-headed Gulls in the British Isles. *Bird Study* 31: 171–186.
- Hudson, A. V. (1989). Interspecific and age related differences in the handling time of discarded fish by scavenging seabirds. *Seabird* 12: 40–44.
- Hudson, A. V., Furness, R. W. (1988). Utilization of discarded fish by scavenging seabirds behind white fish trawlers in Shetland. *J. Zool., Lond.* 215: 151–166.
- Hudson, A. V., Furness, R. W. (1989). The behaviour of seabirds foraging at fishing boats around Shetland. *Ibis* 131: 225–237.
- Hunt, G. L. Jr (1988). The distribution of seabirds at sea: physical and biological aspects of their marine environment. In: van den Elzen, R., Schuchmann, K.-L., Schmidt-Koerig, K. (eds.) *Current topics in avian biology*. Proc. int. 10th E.O.-G. meeting, Verlag der Deutschen Ornithologen-Gesellschaft, Bonn, p. 167–171.
- Huppert, O. (1987). Der Einfluss von Wachstum, Thermoregulation und Verhalten auf den Energiehaushalt der Silbermöwe (*Larus argentatus* Pontoppidan, 1763). Ph.D. dissertation, University of Hamburg.
- Joyd, C., Tasker, M. L., Partridge, K. (1991). The status of seabirds in Britain and Ireland. Poyser, London.
- Markkinnen, G. B., Crutcher, L. C. (1987). The temporal and geographical distribution of continental Black-headed Gulls *Larus ridibundus* in the British Isles. *Bird Study* 34: 1–9.
- Nordhuis, R., Spaans, A. L. (1992). Interspecific competition for food between herring *Larus argentatus* and lesser black-backed gulls *L. fuscus* in the Dutch Wadden Sea area. *Ardea* 80: 115–132.
- Ryan, P. G., Moloney, C. L. (1988). Effect of trawling on bird and seal distributions in the southern Benguela region. *Mar. Ecol. Prog. Ser.* 45: 1–11.
- Sidwell, V. D. (1981). Chemical and nutritional composition of fishes, whales, crustaceans, mollusks and their products. NOAA-TM-NMFS-F/SPO-11, U.S. Department of Commerce, Washington, DC.
- Sokal, R. R., Rohlf, F. J. (1981). *Biometry: The principles and practice of statistics in biological research*, 2nd edn. Freeman, New York.
- Swennen, C., Duxson, P. (1977). Size of food objects of three fish-eating seabird species: *Uria aalge*, *Alca torda*, *Fratercula arctica* (Aves: Alcidae). *Neth. J. Sea Res.* 11: 92–98.
- Tasker, M. L., Webb, A., Hall, A. J., Pienkowski, M. W., Tanglew, D. R. (1987). Seabirds in the North Sea. Final report of phase 2 of the Nature Conservancy Council Seabirds at Sea Project November 1983–October 1986. Nature Conservancy Council, Peterborough.
- Vaak, G., Prater, J., Hartwig, F. (1989). Long term population dynamics of breeding bird species in the German Wadden Sea area. *Helgoländer Meeresunters.* 43: 352–365.
- Wahl, T. R., Hennemann, T. (1975). Seabirds and fishing vessels: co-occurrence and attraction. *Condor* 81: 390–396.
- Warless, S., Hains, M. P. (1992). Activity budgets, diet and breeding success of Kittiwakes *Rissa tridactyla* on the Isle of May. *Bird Study* 39: 145–154.
- Wiens, J. A. (1984). Modelling the energy requirements of seabird populations. In: Whitlow, G. C., Rahn, H. (eds.) *Seabird energetics*. Plenum Press, New York, p. 255–284.

This article was submitted to the editor

Manuscript first received April 21, 1993

Revised version accepted November 20, 1993