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An evaluation of the distribution and scavenging habits of northern fulmars (*Fulmarus glacialis*) in the North Sea

Kees (C. J.) Camphuysen and Stefan Garthe

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Northern fulmars (*Fulmarus glacialis*) are abundant scavengers at fishing vessels in the North Sea. However, despite their abundance and apparent feeding success at (some) fishing vessels, the contribution of discards and offal to their food intake cannot be fully estimated in the absence of less easily gathered data on natural foods. Direct study of fulmar diet has failed to determine the relative importance of discards and offal in the diet. In this paper, the feeding ecology of, and the importance of fishing activities for, fulmars across the whole North Sea is evaluated using results from cruises of fishery research vessels and also observations from a commercial beam trawler. Fulmar and fishery distribution, prey selection and feeding success of scavenging birds, and the relationship of fulmar distribution with hydrographic parameters are the main topics of this study. We found that: (1) fulmars were most abundant in regions of the North Sea where the supply of fishery waste was comparatively low; (2) hydrography predicts fulmar distribution better than fisheries; (3) fulmars at fishing boats obtain discarded offal in proportion to their numerical abundance, but obtain relatively small amounts of discarded roundfish; (4) roundfish are easily robbed from fulmars, and that a marked decline in feeding success in autumn and winter might be attributed to increasing numbers of herring gulls (*Larus argentatus*) at the trawl; and (5) fewer than 50% of the fulmars in the North Sea can be fully supported by fishery waste. These results indicate that, although fulmars clearly profit from fishery waste, fishing activities are not an important determinant of their distribution on a North Sea scale.

Key words: competition, consumption, diet, discards, distribution, fisheries, *Fulmarus glacialis*, hydrography, northern fulmars, North Sea, prey selection.

C. J. Camphuysen: Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands. S. Garthe: Institut für Meereskunde, Düsternbrooker Weg 20, 24105 Kiel, Germany and Institut für Vogelforschung ''Vogelwarte Helgoland'', Inselstation, P.O. Box 1220, D-27494 Helgoland, Germany. Correspondence to C. J. Camphuysen: tel: +31222369488; fax: +31222319674; email: camphuys@nioz.nl

Introduction

Several studies have demonstrated a strong affinity between northern fulmars (*Fulmarus glacialis*) and fishing vessels (Fisher, 1952; Rees, 1963; Wahl and Heinemann, 1979). Today, fulmars are among the most abundant of scavenging seabirds at fishing vessels in the North Sea and in the NE Atlantic (Camphuysen, 1993a; Camphuysen *et al.*, 1995). From studies of scavenging seabirds at whitefish trawlers around Shetland, fulmars were ranked at the apex in the clear dominance hierarchy observed, being able to obtain ''the choicest pickings'' (i.e. fish livers or the entire offal; Furness *et al.*, 1988; Hudson and Furness, 1988, 1989). Tasker *et al.* (1987) concluded that fishing activities were an important determinant of fulmar distribution in the North Sea at certain times of year. More recent studies, often at different scales, were less conclusive and suggested that, although fulmars were evidently attracted in vast numbers by some fishing vessels, the spatial distribution of the main fisheries and fulmars apparently did not match very well (Camphuysen *et al.*, 1995; Stone *et al.*, 1995). Also, recent investigations have suggested that the fulmar's position in the dominance hierarchy at fishing vessels around Shetland may not be so high in other parts of the North Sea (Camphuysen, 1993b; Garthe, 1993; Garthe and Hüppop, 1993, 1994; Camphuysen, 1994a). Hence, despite the abundance and apparent feeding success of fulmars at some fishing vessels, the relative importance of discards and offal in their diets cannot be estimated in the absence of less easily gathered data on natural food resources.

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In this study, the feeding ecology and the importance of fishing activities for fulmars in the North Sea is evaluated. If human fishing activities play a major role in the ecology of fulmars, one might expect positive correlations between fisheries distribution and fulmar numbers at sea. If offal and discards are the most important food source, areas where discards are available in the greatest quantities should be more profitable and would be attractive for fulmars. If, however, more natural prey is preferred, or available at lower cost in certain areas, the distribution patterns of fishing fleets and fulmars may not match very well. Using the same methods as Hudson and Furness (1988, 1989), but in different seasons and different areas of the North Sea, the success of scavenging fulmars at fishing vessels was examined. We studied: (1) the position of fulmars in the dominance hierarchy behind fishing vessels (e.g. vulnerability to kleptoparasitism); (2) feeding success; and (3) consumption of discards and offal. We hypothesized that ‘‘scavenging success’’ of fulmars is high in areas where they numerically dominate at fishing vessels (e.g. in summer around the Shetland Islands), but low if larger numbers of other scavengers occur (e.g. in the southern North Sea). The quantities and the energetic value of discards produced by commercial fisheries in different parts of the North Sea were assessed and compared with the intake of discards by, and the energetic requirements of, fulmars in the North Sea. This allowed the estimation of the number or proportion of fulmars being sustained by fishery waste in the North Sea, given the amounts of discards produced in different areas, the total number of fulmars at sea and the consumption rates of discards and offal at fishing vessels.

Methods

The geographical focus of the study was the entire North Sea area (51–62°N, 4°W–10°E), divided into seven regions (Fig. 1). As rather few discard experiments were carried out in the Skagerrak (region Sk), the data from these were omitted from the analysis. The main aspects of this study were: (1) the spatial distribution, numbers and types of fishing vessels at sea; (2) the spatial distribution, quantities and energetic value of discards and offal produced by commercial fisheries; (3) the spatial distribution and numbers of fulmars at sea; (4) prey selection and consumption (%) of discards by fulmars at fishing vessels; (5) the inter- and intraspecific interactions of scavenging fulmars; and (6) the degree of correlation of certain hydrographic features (e.g. salinity, water temperature, stratification) or distance to the coast with fulmar distribution at sea.

The distributions of fishing vessels and fulmars were studied simultaneously from research vessels carrying out the International Bottom Trawl Survey (IBTS) in January–February 1993, May–June, August–September, and October–November (Camphuysen *et al.*, 1995). While steaming between trawling stations, observers on the top-deck counted seabirds within a 300 m wide strip-transect (90° forward and on one side of the ship), including ‘‘snapshot’’ counts of flying birds (Tasker *et al.*, 1984). From these counts, seabird densities were calculated ($n\ km^{-2}$). The surveys included snapshot counts of fishing vessels within 3 nautical miles around the ship at regular intervals (using radar in combination with the naked eye to identify observed reflections) (see Camphuysen *et al.*, 1995). Steaming fishing vessels (i.e. those not fishing) were not recorded as ‘‘fishing vessels’’ and were therefore not included in the analysis of fisheries distribution. Estimates of total numbers of fishing vessels in the North Sea were derived from these snapshot counts during the IBTS. Estimates of total numbers of fulmars at sea were derived from a more extensive database, the European Seabirds at Sea (ESAS) database (Stone *et al.*, 1995). The numbers of fulmars and other scavengers in flocks associating with (active) commercial fishing vessels were estimated whenever a ship was close enough to allow identification of the species ($n=272$ commercial fishing vessels during these surveys; Camphuysen *et al.*, 1995).

Counts of scavenging seabirds assembling around the ship during hauling and during sessions of experimental discarding of fish and offal were made. The maximum numbers of birds present at any stage of the haul were recorded and used for distribution analysis. Temperature (°C), salinity (ppt) and depth (m) profiles of the water were obtained using a Sea Link CTD probe, from trawling stations to the south of 58°N latitude worked by RV ‘‘Tridens’’. Water with >1 deg C difference between surface and bottom temperatures was regarded as thermally stratified. Surface salinities were categorized as high (>34.5 ppt), intermediate (32.0–34.5 ppt) and low (<32.0 ppt).

The proportion of discards and offal consumed, prey selection, feeding behaviour, and intra- and inter-specific competition among scavenging seabirds were studied aboard the same fisheries research vessels as the counts described above (Camphuysen *et al.*, 1995), on a commercial beam trawler in summer 1993 in the southern North Sea (Camphuysen, 1993b, 1994b), and aboard German research vessels in the central and northern North Sea in summer 1992 and 1993 (Garthe and Hüppop, 1994) and in the German Bight in October 1993 and July 1994 (Garthe, 1993; Garthe and Hüppop, 1996). A fresh sample of fish, offal and benthic invertebrates was taken from each haul to be used for experimental discarding. In all, 841 discard experiments were carried out (Table 1). Items were identified, fish were measured to the nearest cm in total length and were then thrown overboard. Attempts by seabirds to pick up and

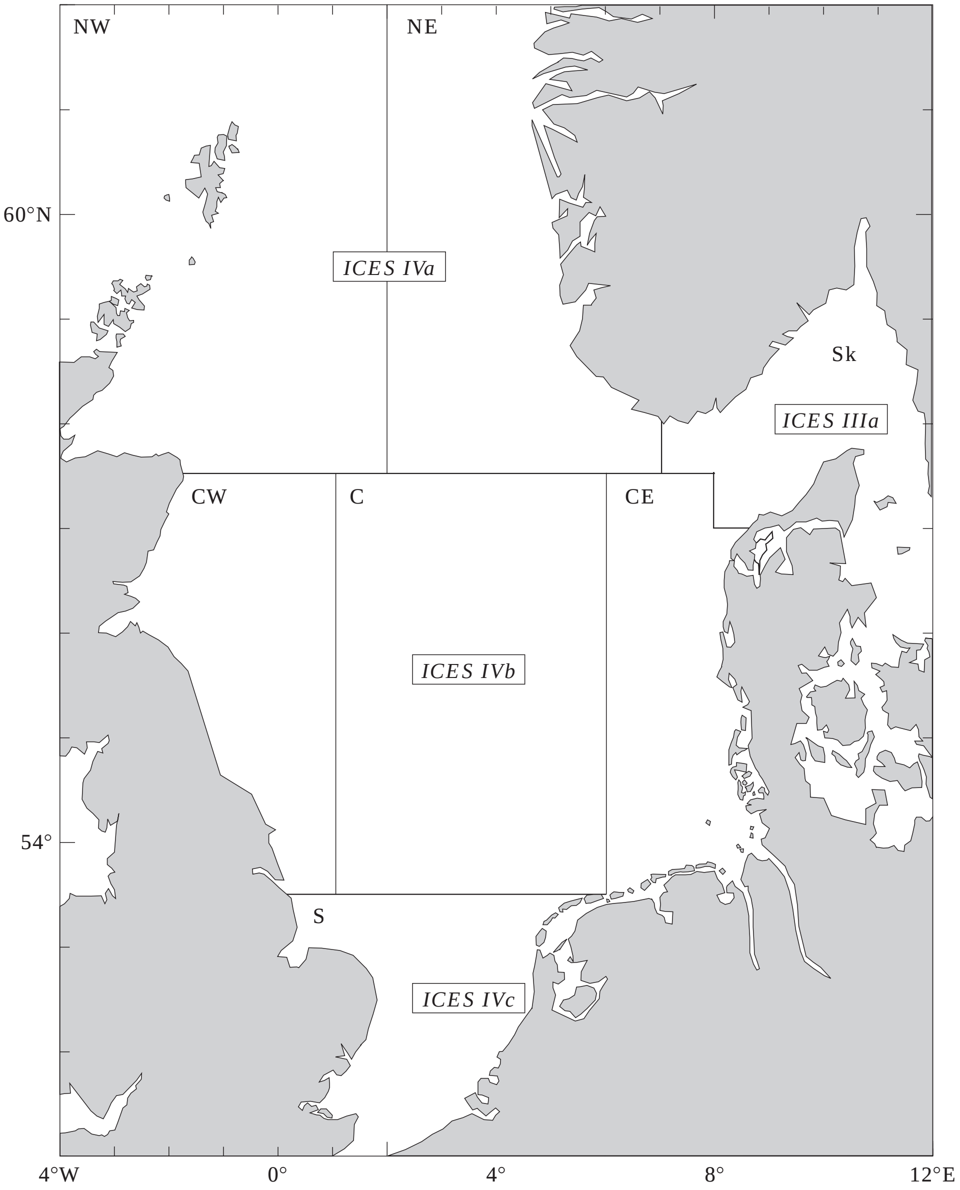


Figure 1. Regions in the North Sea used in the study showing ICES fishing areas IVa–c and IIIa.

swallow the item were recorded on tape, noting whether the item was eaten, dropped or stolen. If it was dropped or stolen, the same notes were made for the second and subsequent birds, until the item was finally lost (by sinking) or swallowed. The frequency with which experimentally discarded items were stolen by fulmars from other seabirds, divided by the number of experimental discards stolen from fulmars by others, was calculated and tabulated as the robbery index (RI). In order to relate the successful consumption of roundfish and offal with the relative abundance of fulmars and other scavengers, we have grouped all discard experiments according to the number of scavengers attracted. Both for fulmars and ‘‘other scavengers’’, each experiment was classified as having attracted ‘‘few’’ (<25 individuals), ‘‘small numbers’’ (26–100 individuals), ‘‘large numbers’’ (101–500 individuals), or ‘‘great numbers’’ (>500 individuals) of scavengers. The result is 16 possible combinations. The observed proportion of discards (and offal) consumed by fulmars was compared with an expected consumption based on the relative abundance of fulmars with respect to other seabirds during the experiments. The overall consumption by fulmars (% of all discards taken by fulmars from all discards consumed by

Table 1. Number of discard experiments per region in each season (studies onboard fishery research vessels and commercial fishing boats combined; n = 841).

Region	Spring	Summer	Autumn	Winter
NW	86	44	23	29
NE	19	17	12	9
CW	63	39	12	12
C	82	92	32	38
CE	70	84	26	15
S	2	13	14	8
Totals	322	289	119	111

scavenging seabirds) and an index of the expected individual feeding success (fraction taken by fulmars divided by the total number of fulmars present) were calculated. These indices were plotted for situations in which fulmars were numerically dominant, occurred in equal numbers or formed a minority at the trawl, in any of the above 16 combinations with other scavengers.

The basis of the statistical analysis that follows is that the probability, p, that a fulmar takes the discarded fish in competition with other scavengers may be given as

$$p=\frac{y}{y+ax^{b}}$$

where y is the number of fulmars and x is the number of other scavengers near the trawler. The parameter a indicates the ‘‘relative competitive strength’’ (rcs) of another scavenger and the parameter b indicates whether the rcs is related to the absolute number of the other scavengers. So, when, for example, $a=2$ and $b=1$, each other scavenger has twice the rcs of the fulmar, implying that when one fulmar and one other scavenger are present, the fulmar has a probability of only 1/3 of getting discards. Reformulating the model in terms of a logit model, which belongs to the class of Generalized Linear Models (Nelder and Wedderburn, 1972; McCullagh and Nelder, 1989), results in:

$$\log\frac{p}{(1-p)}=\log\left(\frac{1}{a}\right)+\log\left(\frac{f}{1-f}\right)+(1-b)\log(x)$$

where f is the fraction of fulmars present $(y/(y+x))$. $\mathrm{Log}(f/(1-f))$ is a so-called offset, which means that it contains no unknown parameter. The parameter values a and b of this basic model were estimated by maximizing the (binomial) likelihood. The basic model was compared with two simpler and two more complicated models. The simplest model is the null model, in which $a=1$ and $b=1$, i.e. where the rcs of other scavengers is equal to one. The model in which the rcs of other scavengers may be different from one, but not related to absolute numbers, i.e. $b=1$, was considered next. In the more complicated models, effects of seasonal (four seasons) and spatial (six regions) factors were also included (with and without the assumption $b=1$). The goodness-of-fit of these four alternative models is indicated by the difference in deviances (divided by the estimate of the dispersion parameter) between each model and the basic model. The dispersion parameters were estimated by the mean deviance of the most complicated model.

Spearman rank correlation coefficients were calculated to test relationships between mean densities of fulmars at sea in seven regions and: (A) the number of fishing vessels km^{-2}; (B) fulmar numbers assembled at the trawl of fishing vessels; and (C) the production of fishery waste (tonnes km^{-2}) in commercial fisheries (offal, roundfish, flatfish, and benthic invertebrates; following Garthe *et al.*, 1996). Seasons used for this paper are winter (Jan–Mar), spring (Apr–Jun), summer (Jul–Sep), and autumn (Oct–Dec).

Significance of all tests was defined as $p \leq 0.05$.

Results

Fulmars and fisheries at sea

Fulmars were abundant and widespread throughout the year, but were particularly numerous in the northwestern two-thirds or three-quarters of the North Sea (regions NW, NE, CW and C, Fig. 2; generalized overall distribution in Fig. 3). In fact, in all seasons, the species avoided a coastal zone in the southern half of the study area, which was narrow off East England and wide in the Southern and German Bights. The Southern Bight was only of some importance in February 1993 after a period of violent storms in the preceding month. In May, concentrations were encountered in the Norwegian and Danish sectors, 4°–8°E longitude. In these areas, several loose groups (scattered birds over wide areas) of hundreds of actively feeding fulmars were observed, apparently feeding on small prey items in the surface layers (swimming and pecking tiny items). In August, moderate to high densities were observed everywhere in the North Sea except in the coastal waters of eastern England, of the Southern Bight and of the German Bight. The central North Sea was of particular importance for fulmars in this season. In November, fulmar distribution was quite uneven, with very high densities in the northern North Sea, and low to moderate densities elsewhere.

The spatial distribution patterns calculated from these four surveys (Fig. 2) matched the patterns found over a long series of years in the North Sea (Stone *et al.*, 1995) and are considered typical for the species. The northwestern half and the central North Sea are of

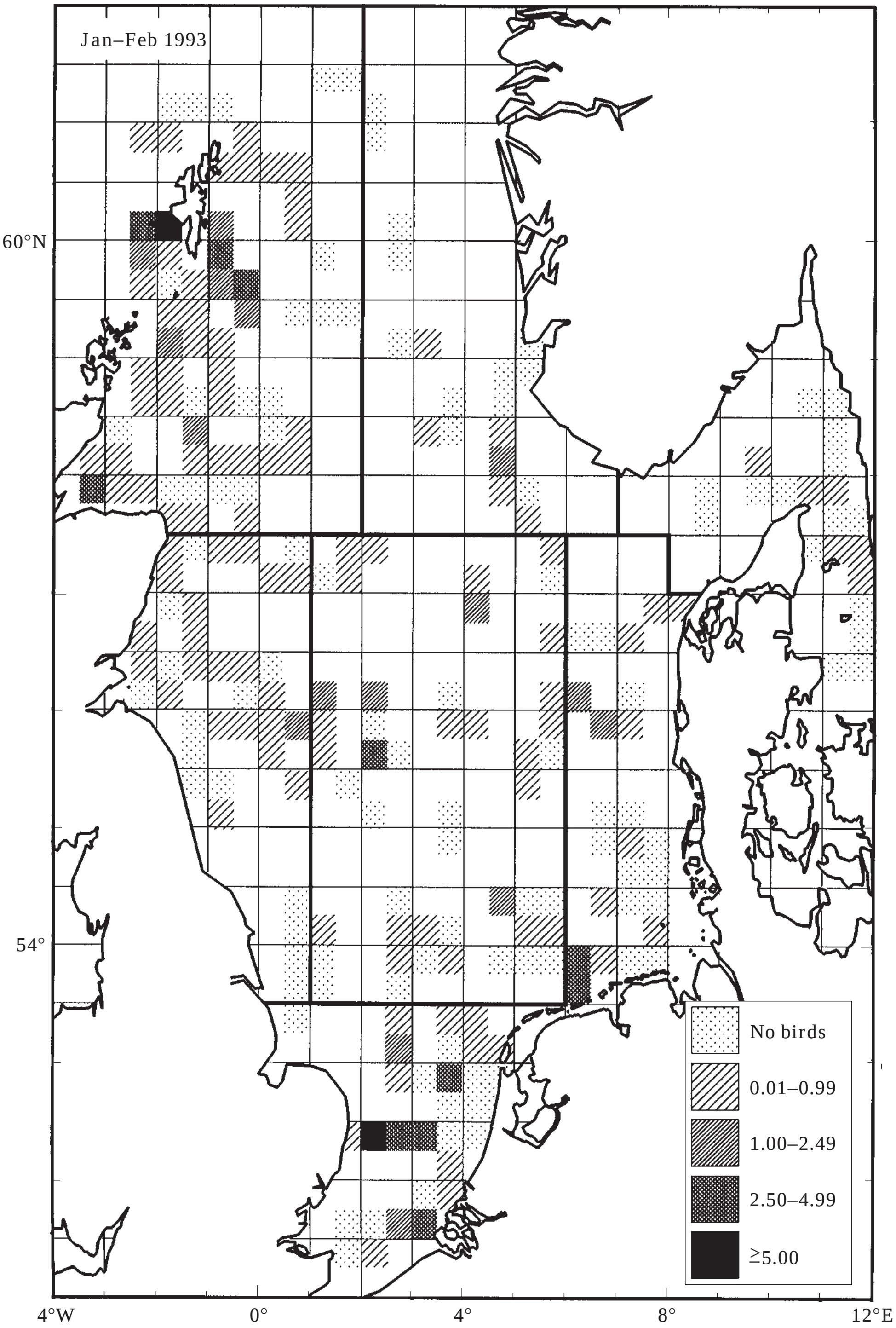


Figure 2. Distribution of fulmars at sea from transect counts (densities per quarter ICES square) in (a) January/February 1993; (b) April/May 1994; (c) August/September 1994; and (d) October/November 1994.

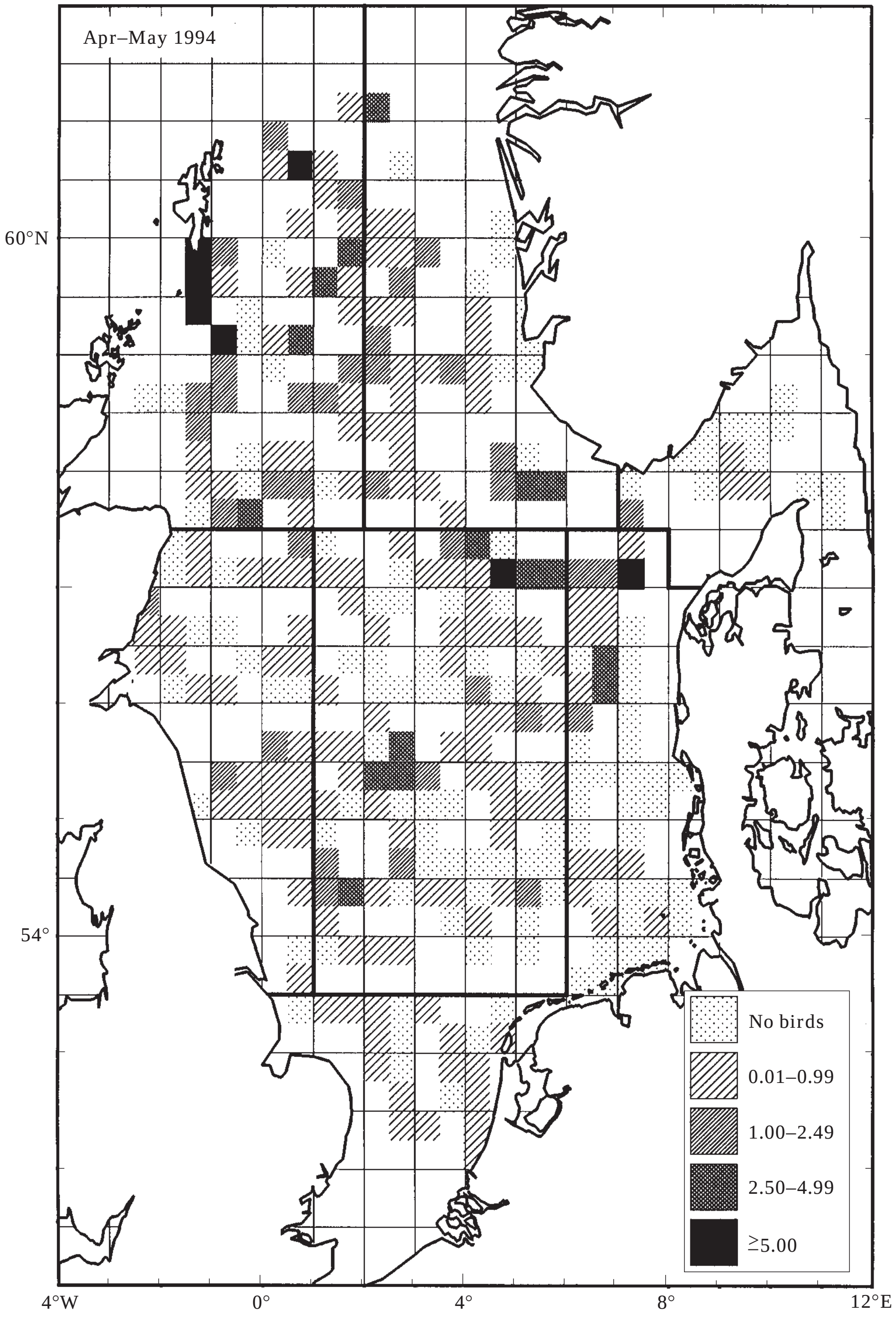
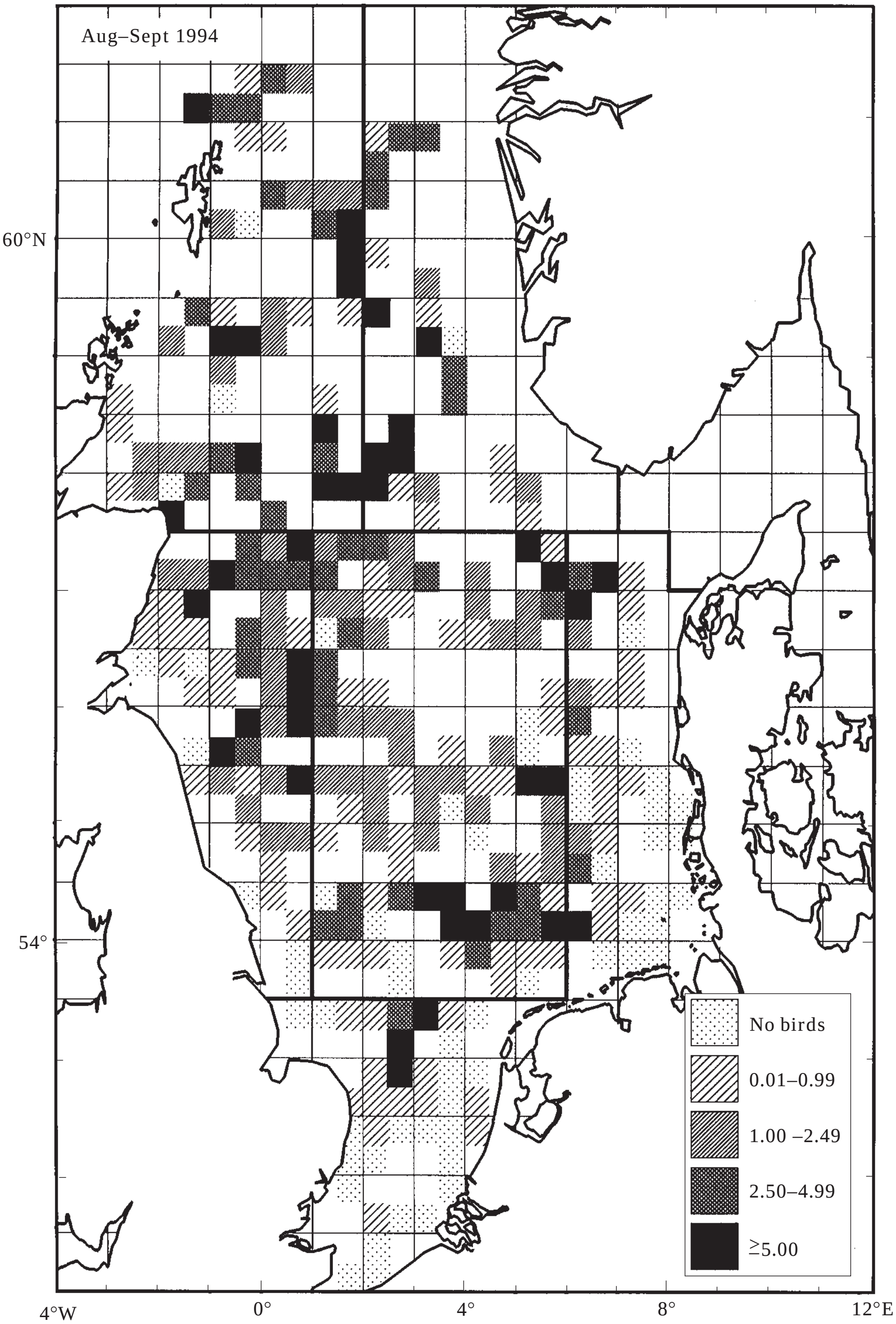

Apr–May 1994
60°N
54°
4°W
0°
4°
8°
12°E
No birds
0.01–0.99
1.00–2.49
2.50–4.99
≥5.00

Figure 2(b).


Aug–Sept 1994
60°N
54°
4°W
0°
4°
8°
12°E
No birds
0.01–0.99
1.00 –2.49
2.50–4.99
≥5.00

Figrure 2(c).

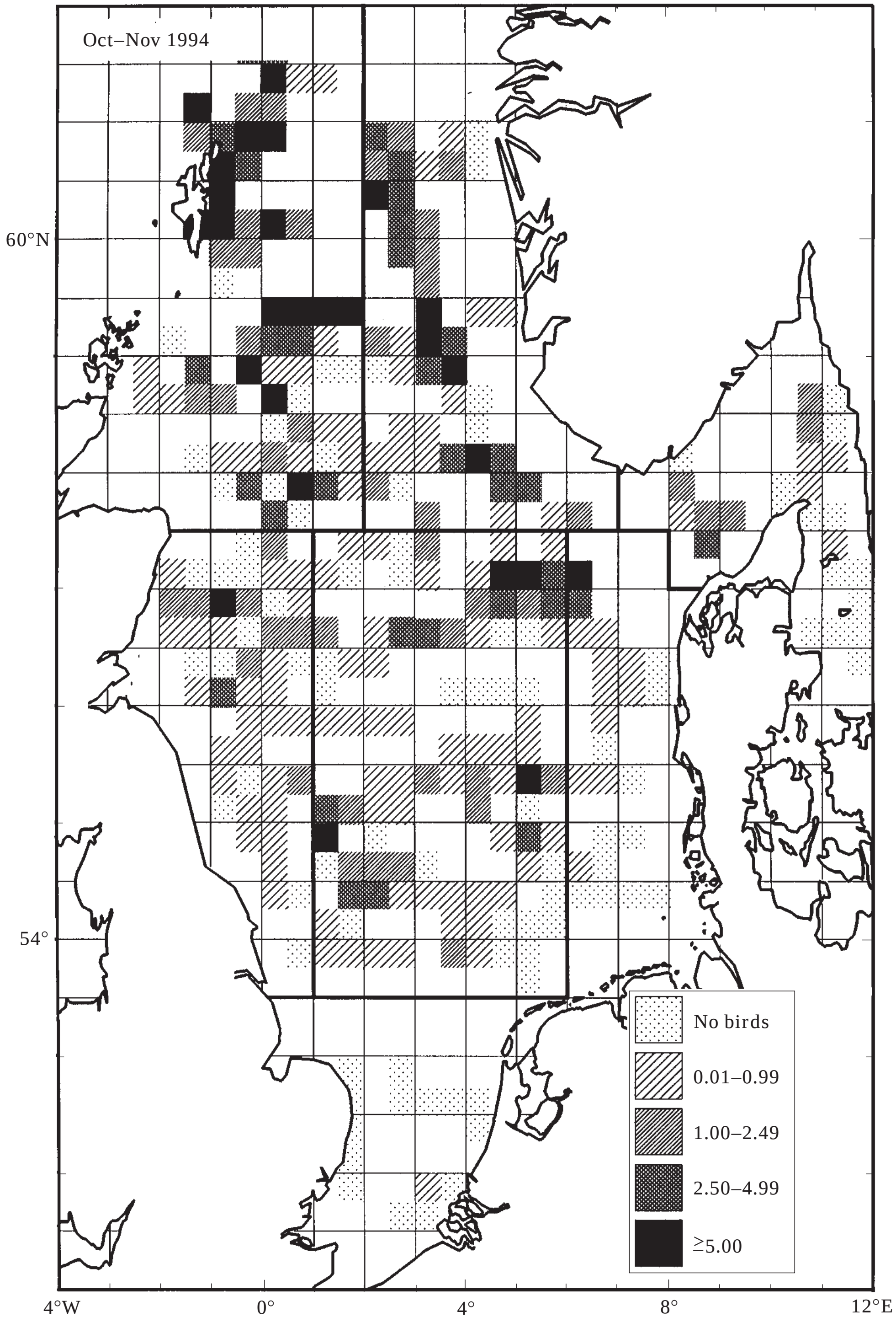

Oct–Nov 1994
60°N
54°
4°W
0°
4°
8°
12°E
No birds
0.01–0.99
1.00–2.49
2.50–4.99
≥5.00

Figure 2(d).

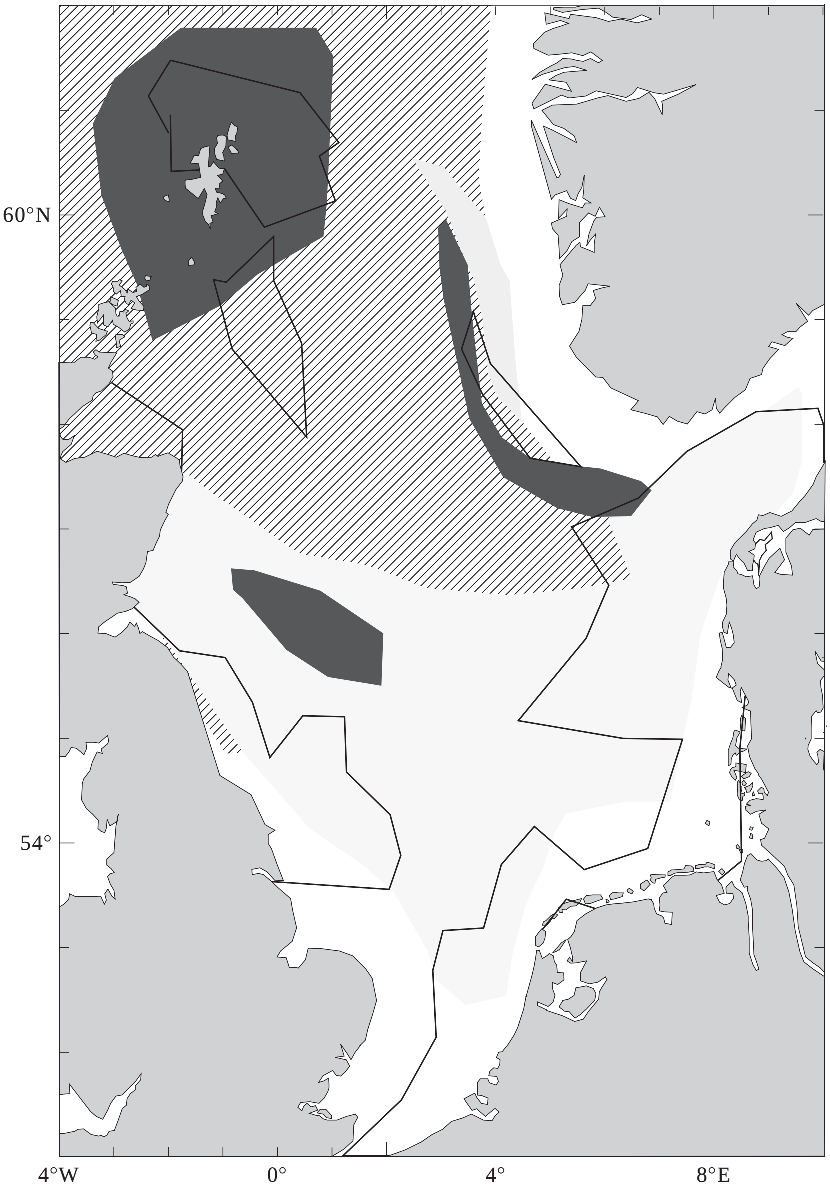


Figure 3. Generalized distribution of fisheries and fulmars in the North Sea from sightings of fulmars and fishing vessels in the ESAS database (unpublished data and Skov *et al.*, 1995). Areas with high densities of commercial fishing vessels are defined by polygons with solid lines. High (dark shading), moderate (light shading), low densities (very light shading) and very low density (blank) areas of fulmars are indicated.

prime importance for the fulmar, whereas the shallow coastal waters, particularly in the south-east, are of lesser importance (Fig. 3). These and earlier investigations point at the western margins of the Norwegian Trench (Norskerenna) as an area of great importance throughout the year, despite the absence of breeding fulmars in most of SW Norway. Stone *et al.* (1995) found even greater numbers in the Skagerrak than we did.

Fishing vessels

The overall densities of active fishing vessels at sea were generally highest in regions CE and S (Table 2), most of which were beam trawlers and shrimpers and set net fishing vessels further to the north. In February 1993, comparatively high densities of fishing vessels were reported in the Southern Bight, the German Bight, off the Danish west coast, off the English east coast, in

Table 2. Estimated total number of commercial fishing vessels in each of the regions at different times of the year and the overall mean density (n km^{-2}) from systematic surveys in 1993 and 1994 onboard fisheries research vessels (Camphuysen *et al.*, 1995) n.d. = no data).

Region	Winter	Spring	Summer	Autumn	Mean	n 100 km^{-2}
NW	340	140	350	200	260	0.17
NE	310	150	420	190	270	0.28
Sk	100	90	n.d.	20	70	0.12
CW	110	90	130	60	100	0.14
C	420	330	210	130	270	0.19
CE	90	160	420	130	200	0.32
S	170	500	200	170	260	0.46
Totals	1530	1460	1740	890	1410	

the Moray Firth, around northern Shetland, and off south-west Norway between Bergen Bank (60°N 3°E) and Eigersundsbank (58°N 5°E; generalized overall distribution in Fig. 3). Areas were classified as having high densities of fishing vessels if more than one active fishing boat was observed per 4 nautical miles (7 km) of steaming. In May 1994, densities of fishing vessels were particularly high in the Southern Bight (S) and at the Little Fisher Bank, around the border of the Danish and Norwegian sectors of the North Sea. In August, except in the central North Sea and in the Southern Bight, densities of fishing vessels were higher than in the other surveys, with scattered moderate to high densities being slightly more widespread than in May. Extensive fisheries occurred off north-west Denmark, south-west Norway (Bergen Bank area) and in the German Bight. In November rather low numbers of fishing vessels were recorded, lower than in any of the other months. In all regions, fewer fishing vessels were at sea than in August and only the northernmost regions held more vessels than in the May survey. Clusters of fishing vessels were present off north-east Scotland, well offshore west of Denmark and off eastern England. In February 1993, it was estimated that just over 1500 fishing vessels were active in the North Sea. The total numbers of fishing vessels, extrapolated from snapshot counts, ranged from nearly 900 boats in November, through 1460 in May, and over 1740 in August (Table 2). Throughout the year, beam trawlers and shrimpers were concentrated in subregions S, CE, and C, while purse seiners, stern and otter trawlers were comparatively numerous in the central and northern North Sea. Pairs of trawlers were widespread. Anchor seiners and set net fishing boats were most numerous off the Danish coast.

Fulmars at the trawl

Fulmars were the most abundant scavengers at the trawl of research vessels in most of the North Sea and during most of the year. Peak numbers assembled at the trawl in each of the surveys ranged between ca. 2000 and 2500. Fulmars were not evenly distributed over the entire North Sea. The largest numbers were usually reported in regions NW, NE, CW and C, whereas moderate to small numbers were found in Sk, CE and S (Fig. 4).

The fulmar was the commonest species seen in association with commercial fishing vessels. Particularly high numbers were observed in the north (3500 as a maximum in NW in February), and occasionally in the central North Sea (2000 as a maximum in C in May). In February, up to 700 fulmars were observed in association with a fishing vessel in the Southern Bight, but otherwise, groups of over 100 fulmars were quite rare in the southern and eastern North Sea and in the Skagerrak. In the central and western half of the North Sea, several hundreds of fulmars at boats were more frequently reported. The observed maxima at fishing vessels were similar to or slightly higher than maxima recorded at the stern of research vessels. The overall picture, although based on a small sample (272 commercial boats), is similar to distribution patterns derived from stern counts at research vessels.

Total numbers of fulmars

Total abundance estimates of fulmars at sea in each of the North Sea regions, based on mean numbers in association with commercial fishing vessels, total numbers of commercial boats and extrapolations from densities of fulmars based on strip-transect counts assessed during the IBTS in 1993 and 1994, varied between virtually none in region S in autumn to over 1 million individuals in region NW in autumn (Table 3). Camphuysen *et al.* (1995) and Van der Meer and Camphuysen (1996) analysed the abundance estimates derived from these four surveys and concluded that the results were conservative. Using estimates derived from the ESAS database (Stone *et al.*, 1995), abundance estimates for fulmars ranged from 1.1 million in February, to 2.1 million in May, 3.7 million in August, and 2.8 million individuals in November.

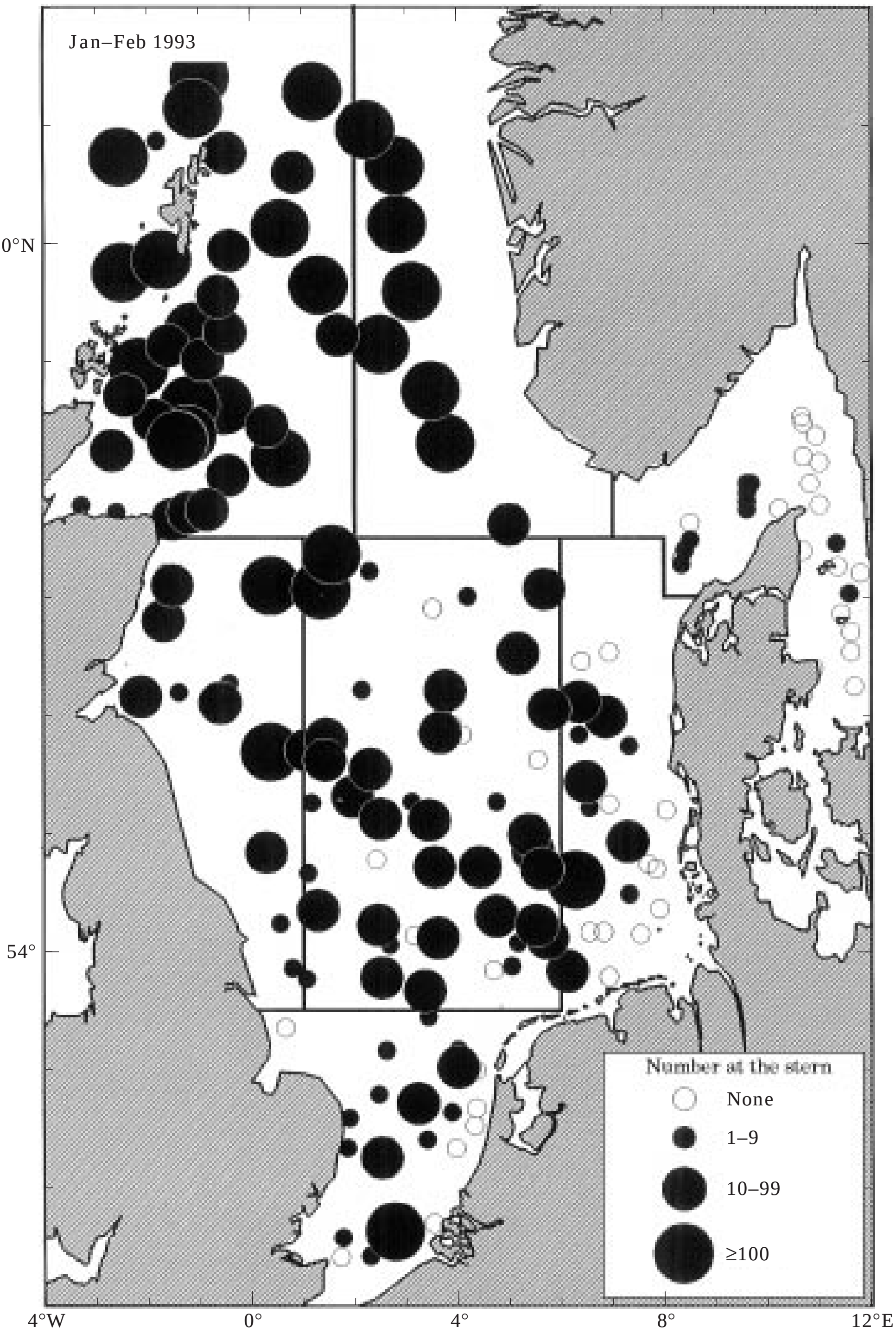


Figure 4. Distribution of fulmars assembled at the stern of research vessels (maximum numbers observed at each haul) in (a) January/February 1993; (b) April/May 1994; (c) August/September 1994; and (d) October/November 1994.

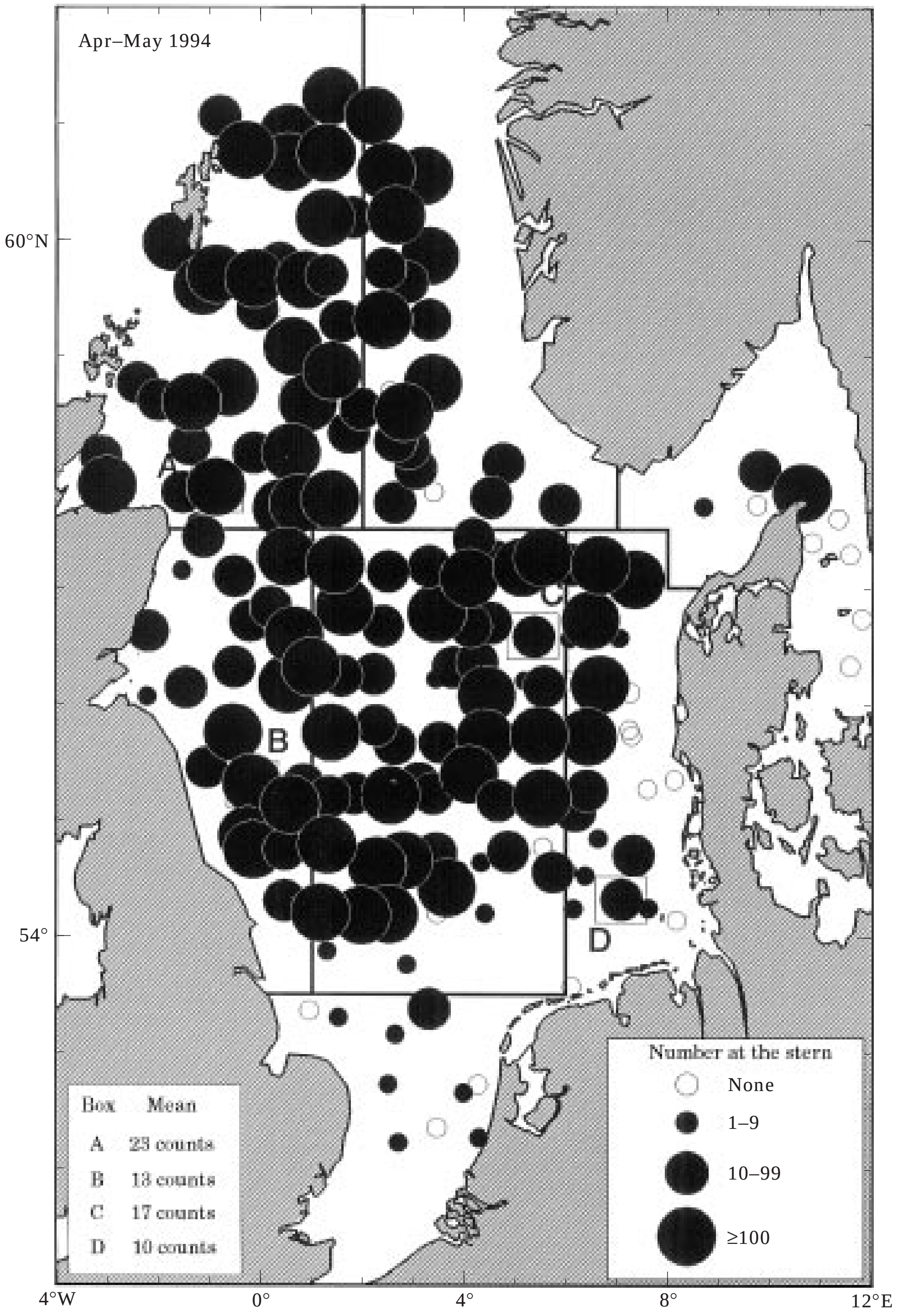

Apr–May 1994
60°N
54°
4°W
0°
4°
8°
12°E
A
B
C
D
Box Mean
A 23 counts
B 13 counts
C 17 counts
D 10 counts
Number at the stern
None
1–9
10–99
≥100

Figure 4(b).

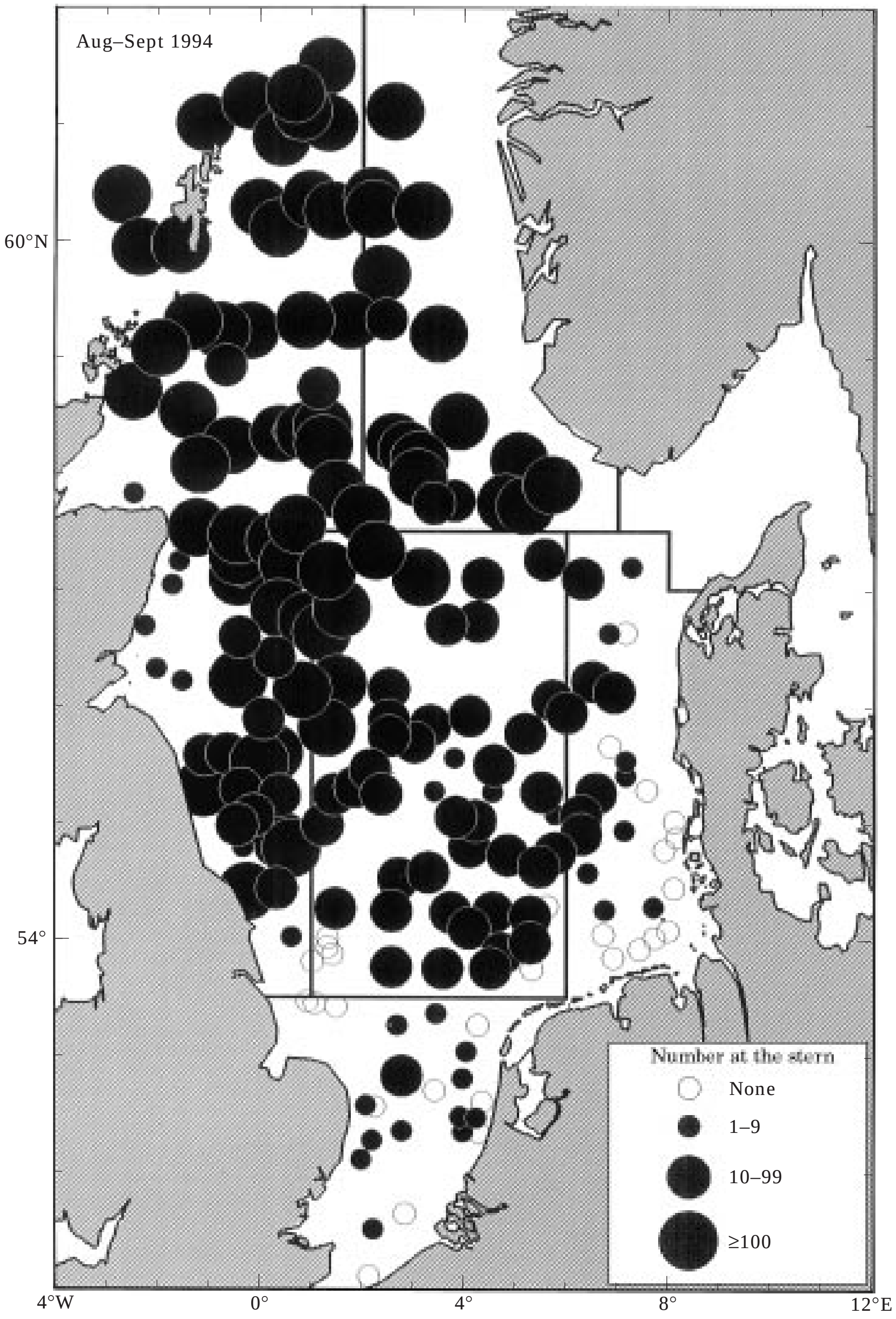

Aug–Sept 1994
60°N
54°
4°W
0°
4°
8°
12°E
Number at the stern
None
1–9
10–99
≥100

Figure 4(c).

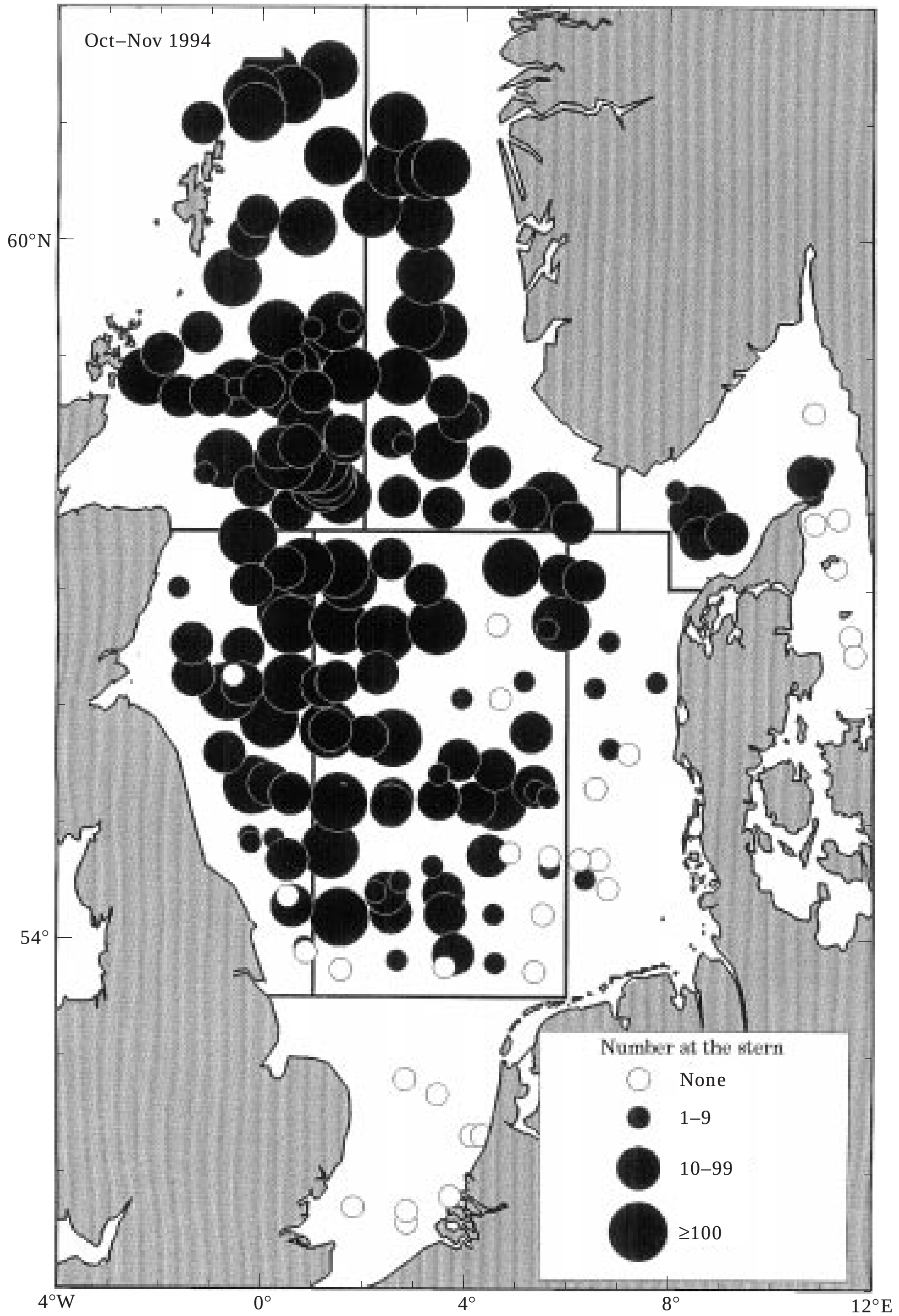

Oct–Nov 1994
60°N
54°
4°W
0°
4°
8°
12°E
Number at the stern
None
1–9
10–99
≥100

Figure 4(d).

Table 3. Estimated total numbers of fulmars in the North Sea (thousands) in each region at different times of the year, calculated from strip-transect counts (n km^{-2} $region^{-1}$) counts of birds associated with commercial trawlers (n $trawler^{-1}$), and trawler counts (trawlers $region^{-1}$) in 1993 and 1994 onboard fisheries research vessels (Camphuysen *et al.*, 1995). Breeding numbers (thousands) on coastal cliffs in each region are given in parentheses (Hunt and Furness, 1996; n.d. = no data).

Region	(Breeding)	Winter	Spring	Summer	Autumn	Mean
NW	(590)	330	300	620	1230	620
NE	(0)	90	120	510	320	260
Sk	(0)	10	10	n.d.	30	20
CW	(29)	40	30	230	50	90
C	—	120	210	410	160	230
CE	(0)	30	160	80	50	80
S	(1)	70	10	60	0	40
Totals	(616)	670	850	1900	1850	1320
ESAS estimate		1100	2100	3700	2800	2400

Fulmar distribution in relation to fisheries and hydrography

On average, fulmar numbers in region NW were two to three times higher than in any of the other regions (Table 3). However, large numbers were observed most of the year in regions NE and C. Compared to the distribution of active fishing vessels, fulmar numbers were always very low in regions S, CE and Sk, low in winter but quite high in summer in NE and C, variable in CW and always very high in NW. Hence, on a crude, whole North Sea scale, there is little relationship between fulmar distribution and that of fishing vessels.

In winter, fulmar densities were positively, but not significantly correlated with trawler densities in each of the seven regions (R_s 0.643, df = 6, $0.1 < p < 0.05$; Table 4). In no other seasons were positive correlations found between fulmar densities and trawler abundance. Camphuysen *et al.* (1995) reported that fulmar numbers associated with beam trawlers were comparatively low compared with other types of fishing vessels. However, overall fulmar densities at sea were not (positively) correlated with densities of other types of fishing vessels (R_s − 0.029, df = 5, n.s.).

Garthe *et al.* (1996) calculated the availability of fishery waste using the same data on trawler abundance and trawler distribution, and included information on

Table 4. (A) Relationships between densities of fulmars at sea in seven regions and the relative abundance of active fishing vessels, and fulmar abundance during experimental discarding (mean numbers assembled at trawl) in winter, spring, summer, and autumn. (B) Relationships between densities of fulmars at sea in six regions (Sk excluded from analysis) and the availability of fishery waste (Garthe *et al.*, 1996). Spearman rank correlation coefficients are shown. Significance levels: n.s. = p > 0.05, * = p < 0.05, ** = p < 0.01, *** = p < 0.001.

(A) Fulmar densities versus		Winter	Spring	Summer	Autumn	Overall
Trawlers km^{-2}	R_S	0.643	0	− 0.085	0	0
	p	n.s.	n.s.	n.s.	n.s	n.s.
Fulmar numbers at trawl	R_S	0.857	0.393	1.000	0.729	0.893
	p	**	n.s.	***	*	**

(B) Fulmar densities versus	R_S	Significance
Availability of all fishery waste (t km^{-2})	− 0.828	*
Specified fractions of fishery waste:		
Availability of offal (t km^{-2})	− 0.770	*
Availability of roundfish discards (t km^{-2})	− 0.428	n.s.
Availability of flatfish discards (t km^{-2})	− 0.942	**
Availability of discarded benthic invertebrates (t km^{-2})	− 0.942	**

Table 5. Presence (%), mean and maximum numbers of fulmars assembled at trawls during 841 sessions of experimental discarding thoughout the North Sea and through the year.

	NW	NE	Sk	CW	C	CE	S	Overall
Presence (%)								
Winter	100	100	43	92	92	40	50	82
Spring	100	100	17	100	99	77	100	93
Summer	100	100		97	95	77	62	90
Autumn	100	100		100	91	42	64	81
Mean								
Winter	229	334	2	46	23	9	54	100
Spring	275	266	0	429	94	26	9	157
Summer	408	442		212	89	16	6	196
Autumn	180	238		69	69	1	8	94
Maximum								
Winter	2000	800	12	240	120	60	385	2000
Spring	1600	1100	2	2500	700	480	12	2500
Summer	2500	1300		800	800	300	50	2500
Autumn	940	700		300	250	15	35	940

the relative distribution of different trawler types and estimated amounts of fishery waste discharged in the respective fisheries. Consequently, fulmar densities at sea were compared with the amount of discards provided (tonnes km^{-2}) in each of the North Sea regions. Strong negative correlations were found between fulmar densities at sea and the availability of different types of fishery waste (Table 4). This suggests that neither the fisheries alone, nor the fishery waste which is produced, are primary determinants of fulmar distribution at sea.

During experimental discarding from commercial fishing vessels and fishery research vessels in different parts of the North Sea, fulmars assembled at the stern on 754 (89.7%, n=841) occasions. Fulmar presence was consistently very high in regions NW, NE, and CW, slightly lower in C and lower again in Sk, CE and S (Table 5). Similarly, mean numbers assembled at the trawl were highest in NW and NE, slightly lower in CW and lower again in Sk, CE, and S. Both presence and mean numbers of fulmars assembled at the trawl were positively correlated, often highly significantly, with the densities of fulmars at sea in each of the regions (Table 4), except in spring (i.e. mainly May observations). This would indicate that the number of fulmars attracted to a fishing vessel is a function of their overall abundance at sea.

In the central and southern North Sea (regions CW, C, CE, and S; May and August surveys) in summer, fulmars were particularly numerous to the north of 54°N and greater than 100 km from the coast (Table 6). High numbers of fulmars attracted to fishery research vessels coincided with thermally stratified water of comparatively high salinity (Fig. 5). As a result, a fishing vessel leaving the German Bight or the English east coast and travelling towards the central North Sea might attract large numbers of fulmars at trawls when relatively saline, clear, and (in summer) thermally stratified waters

Table 6. Mean number of fulmars assembled (mean, s.d., and sample size) at trawls during session of experimental discarding in the central and southern North Sea (regions CW, C, CE, and S) in relation to latitude, distance to the coast, thermal stratification, and salinity. Data from RV ‘‘Tridens’’, May and August 1994.

		May			August		
		Mean	s.d.	n	Mean	s.d.	n
Latitude (°N)	>54.5°	57.4	116.4	27	65.0	124.8	23
	<54.5°	12.8	18.9	20	41.8	12.6	17
Distance to land (km)	>100	68.5	133.5	20	41.8	139.8	17
	<100	16.2	21.5	27	9.3	15.5	23
Thermal stratification	Stratified	53.7	117.3	27	63.0	119.6	25
	Mixed	17.9	22.6	20	6.3	9.4	15
Surface salinity	>34.5	60.5	123.5	24	74.8	141.9	3
	32.0–34.5	18.0	19.9	16	19.8	31.6	20
	<32.0	9.7	15.7	7	0.7	1.2	17

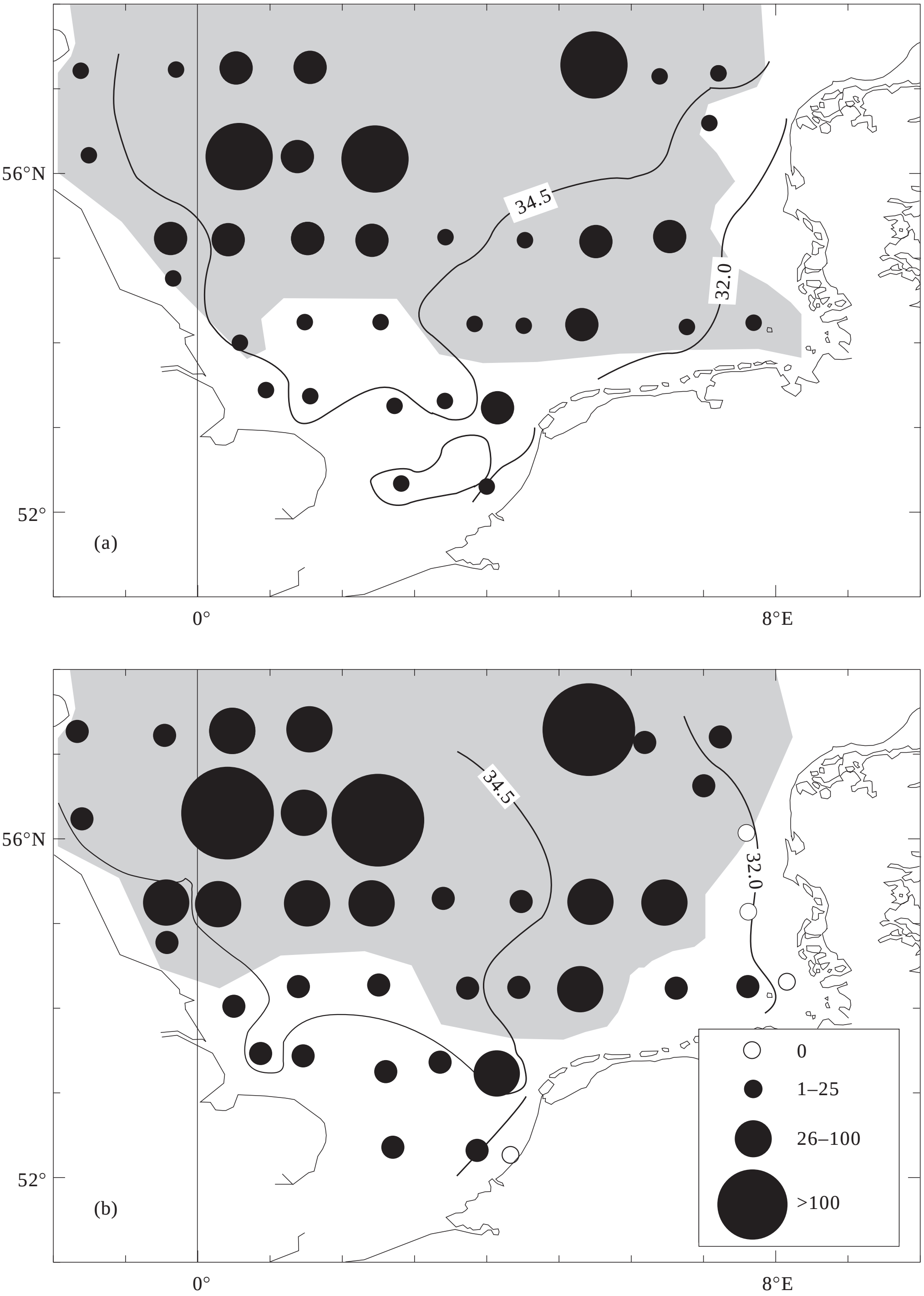


Figure 5. Numbers of fulmars recorded during fishing in the southern North Sea in relation to hydrographic features (salinity and thermal stratification) in May (top) and August (bottom) 1994. The shaded areas represent regions where thermal stratification occurred. Lines indicate surface salinity.

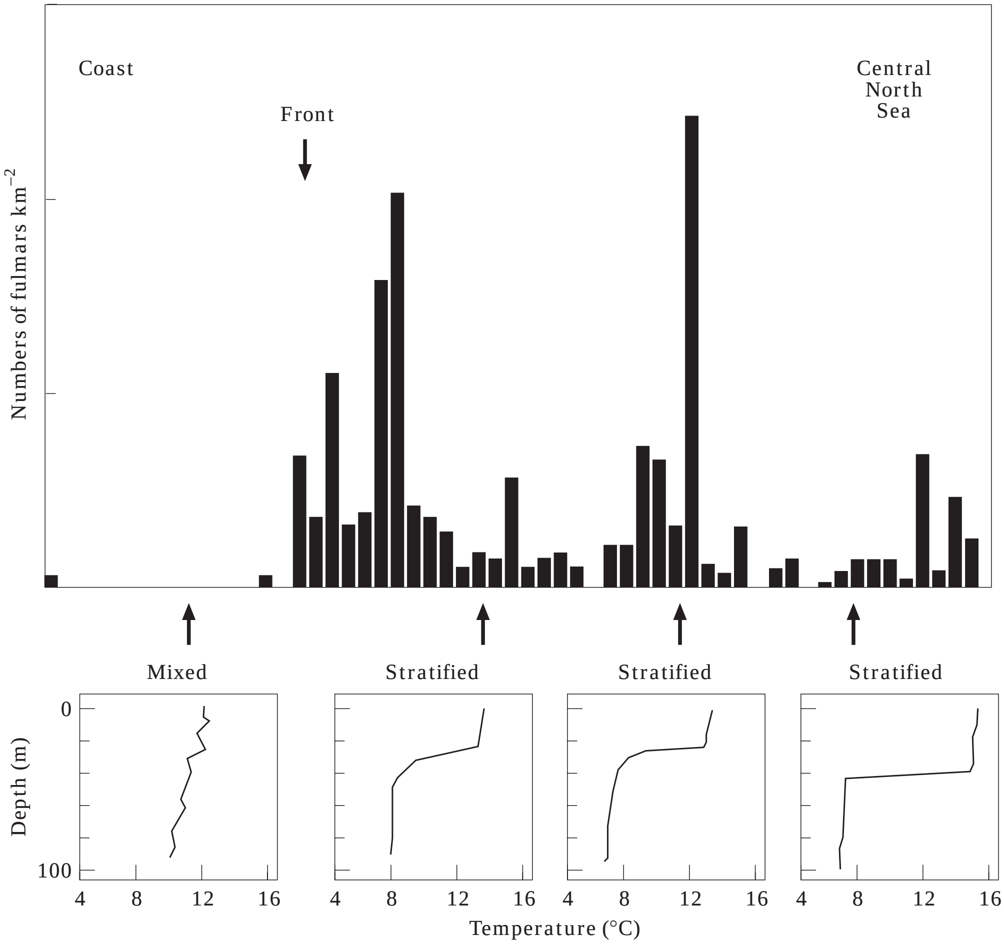


Figure 6. Densities of fulmars (km^{-2}) at sea on a transect perpendicular to the Scottish coast, in relation to water masses and the approximate position of the Aberdeen frontal zone. Thermally stratified water masses were observed on the seaward side of the front, whereas mixed waters occured on the landward side (observations from RV ''Tridens'', August 1995). Bird densities were plotted per 10 min of observation. Temperature profiles were obtained at fishing stations.

were reached (Table 6). In the absence of thermal stratification in winter, fulmars were attracted to fishing vessels in most of the North Sea, but northerly and offshore components to their distribution were still obvious (Fig. 3).

The results of transect counts revealed a similar distribution pattern and also clear correlations with certain hydrographic features. For example, relatively high densities of fulmars throughout most of the year were found in ''Atlantic'', ''Northern'' and ''Central North Sea water'' (Lee, 1980). Boundaries between certain (coastal) areas with low densities and (offshore) areas with high densities in the southern half of the North Sea were usually abrupt and closely matched the borders between homohaline areas and areas that are stratified thoughout the year (Lee, 1980; Garthe and Hüppop, 1995; examplified in Fig. 6). Clear patterns with such boundaries, often matching the positions of oceanic fronts, were found along the British east coast (e.g. Aberdeen Front, Flamborough Head Front) and in the Southern Bight (Frisian Front).

Feeding behaviour at fishing vessels

Fulmars that were attracted to fishing vessels would normally fly around the vessel in wide circles, alight on the water at some distance and then approach the vessel as soon as the net appeared near the surface. Fulmars landed near, and rapidly swam towards, floating fish, threatening and attacking other birds. Small roundfish were normally swallowed whole, whereas larger roundfish were usually pecked to reach the liver and intestines. Groups of fulmars tended to compete over single fish while ignoring large quantities floating nearby. In order

Table 7. Benthic invertebrates (B), cephalopods (C), elasmobranchs (E), flatfish (F), jellyfish (J), offal (O), and roundfish (R) of which at least 100 items or individuals were offered in the presence of fulmars and the proportion of these consumed by the birds. Data from all surveys combined.

G	Scientific name	Offered	Consumed	% by fulmars
B	*Aphrodite aculeata*	113	1	1
B	*Palaemon serratus*	112	32	29
B	*Corystes cassivelaunus*	228		0
B	*Liocarcinus holsatus*	176		0
B	*Pagurus bernhardus*	158	1	1
B	*Asterias rubens*	1332	1	0
B	*Astropecten irregularis*	606		0
B	*Ophiura* spp.	422		0
B	Other species	289	7	2
C	All species combined	86	19	22
E	All species combined	54	8	15
F	*Pleuronectes platessa*	470		0
F	*Limanda limanda*	3197	7	0
F	*Microstomus kitt*	196		0
F	*Hippoglossoides platessoides*	730	51	7
F	*Solea solea*	144	1	1
F	Other species	128	2	2
J	All species combined	10		0
O	Offal	7968	4533	57
R	*Clupeoid* spp.	144	36	25
R	*Clupea harengus*	7826	1946	25
R	*Sprattus sprattus*	2848	555	19
R	*Argentina sphyraena*	340	201	59
R	*Gadus morhua*	1411	270	19
R	*Melanogrammus aeglefinus*	5657	1542	27
R	*Merlangius merlangus*	10 082	2213	22
R	*Micromesistius poutassou*	101	58	57
R	*Trisopterus minutus*	380	25	7
R	*Trisopterus esmarkii*	6025	2225	37
R	*Trisopterus luscus*	476	1	0
R	*Trigla lucerna*	171	2	1
R	*Eutrigla gurnardus*	1915	34	2
R	*Agonus cataphractus*	128	1	1
R	*Trachurus trachurus*	489	28	6
R	*Ammodytes* spp.	1637	892	54
R	*Hyperoplus lanceolatus*	249	105	42
R	*Callionymus lyra*	296	7	2
R	*Scomber scombrus*	906	66	7
R	Other species	660	207	31

to obtain sinking discards, fulmars were seen to dive up to a few metres deep, but normally only floating discards were consumed.

The numbers of fulmars associating with trawlers varied depending on fishing activity. Large numbers approached when ships produced discards while stationary (Camphuysen *et al.*, 1993) but numbers reduced immediately when steaming or towing was resumed. Fulmars were generally unable to pick up discards while on the wing and this was a serious disadvantage for them when competing with gulls, especially when fishing vessels such as beam trawlers produced a steady trickle of discards and offal while steaming or towing (Camphuysen, 1993b).

Prey selection at the trawl

In total, 58 160 fish, offal particles, squid, jellyfish and benthic invertebrates were offered during sessions of experimental discarding in the presence of fulmars. Of these main food types, variable proportions were consumed, suggesting strong preferences for certain species (Table 7) and prey size (Fig. 7). High proportions of offal and slender, small, non-spiny roundfish were swallowed by fulmars. Flatfish, large spiny roundfish such as red gurnard (*Trigla lucerna*) and grey gurnard (*Eutrigla gurnardus*), and benthic invertebrates were usually ignored, even if there was no alternative available.

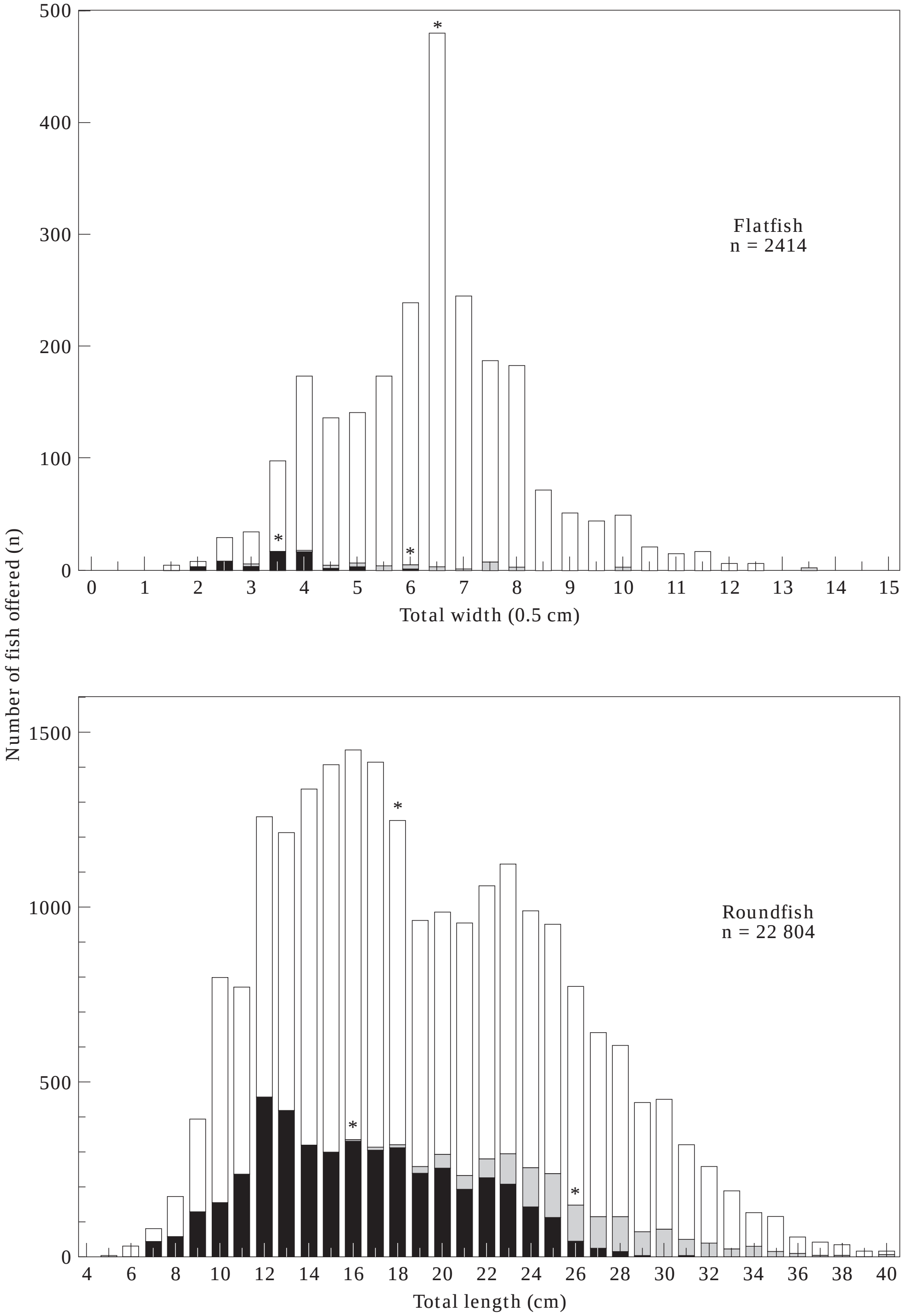


Figure 7. Width of flatfish and length of roundfish consumed (solid) or pecked (shaded) by fulmars. Offered numbers (n = 2412 flatfish, 22 804 roundfish) refer to discard experiments aboard fisheries research vessels in which fulmars assembled at the stern. Medians are indicated by *. □ offered; ▨ pecked; ■ consumed.

Table 8. Numerical dominance (% of all groups of scavengers) of fulmars at trawlers in the North Sea. Sample sizes are given in parentheses.

Region	Spring	Summer	Autumn	Winter
NW	46% (171)	74% (172)	13% (40)	11% (142)
NE	54% (37)	99% (67)	32% (28)	11% (19)
CW	31% (127)	51% (166)	3% (35)	4% (74)
C	32% (186)	49% (292)	11% (133)	3% (234)
CE	11% (157)	10% (186)	0% (41)	1% (105)
S	2% (138)	4% (106)	1% (140)	3% (308)

Clearly, fulmars had difficulty handling and swallowing larger gadids and were more successful at swallowing small gadids such as silvery pout (*Gadiculus argenteus*) and Norway pout (*Trisopterus esmarckii*), and also blue whiting (*Micromesistius poutassou*), three species with a northerly distribution. The median total length of roundfish such as herring (*Clupea harengus*) and whiting (*Merlangius merlangus*) swallowed by fulmars was 16 cm and the maximum 33 cm. The median size taken by fulmars was only slightly less than the median offered to them. Fulmars did not seem unable to swallow roundfish due to anatomical constraints, as suggested by Hudson and Furness (1988), but large fish were usually ignored if sufficient alternative prey was available.

Flatfish up to 6 cm in body width were succesfully swallowed by fulmars, but in very small amounts. The median width of flatfish consumed by fulmars was 3.5 cm, only half the median width offered.

Benthic invertebrates consumed by fulmars included six aesop prawn (*Pandalus montagui*), 32 common prawn (*Palaemon serratus*) and an occasional starfish (*Asterias rubens*), hermit crab (*Pagurus bernhardus*) or sea-mouse (*Aphrodite aculeata*). The results suggest, therefore, that only roundfish discards and offal are consumed by fulmars in significant quantities. Only these will be considered further.

Intra-specific and inter-specific competition at the trawl

Large pieces of offal, particularly large cod-livers, were torn by rapidly growing flocks of fighting fulmars. However, most offal particles were small and easily swallowed by individual fulmars, and so were not usually stolen from each other in the way fish were. In areas of high fulmar density, large groups formed and most fights for discards and offal were between individuals of the same species. Most roundfish discards that were lost by fulmars due to kleptoparasitism were stolen by other fulmars (77.9%, $n=7368$). Fish that were simply dropped after being handled but later picked up by another fulmar without fighting had a mean length of 21.7 cm. These fish were significantly smaller than fish that were stolen from one fulmar by another (mean length lost by kleptoparasitism 24.4 cm; $Z=-8.773$, $n_1=276$, $n_2=5738$, $p<0.001$). Individual roundfish, initially picked up by a fulmar, were handled by up to 24 scavengers successively. Small roundfish (<10 cm) were usually swallowed instantly (on average 0.2 birds handling the fish, maximum 2), whereas larger fish were handled by an increasing number of scavenging birds (10–19 cm, mean 0.15, max 15 scavengers; 20–29 cm, mean 0.84, maximum 24; 30–39 cm mean 0.98, max 19; ≥40 cm mean 1.06, max 5). Fulmars handling roundfish discards were robbed on 1630 occasions by other seabirds and obtained only 465 items by robbery from other species ($RI=0.3$). Hence, fulmars were highly vulnerable to kleptoparasitism, and were consistently the second lowest in the hierarchy in each region, in each of the surveys, and for each of the categories of discarded fish. Of the discards stolen from fulmars ($n=1630$), most were taken by gannets (57.4%) and great black-backed gulls (13.3%). Most of the roundfish discards taken by fulmars from other seabirds ($n=465$), were taken from kittiwakes.

Large groups of scavenging fulmars, as well as groups in which fulmars were numerically dominant over other scavengers, occurred most frequently (>30% of all observed groups of scavenging seabirds) in regions NW, NE, CW and C in spring and summer, and in region NE in autumn (Table 8). Fulmars clearly had a greater success rate during discard experiments in which they numerically dominated in the scavenging flock (Fig. 8). The relationship between the frequency of occurrence (%) of such flocks at fishing vessels and the consumption of roundfish and offal (%) was highly significant (roundfish $r^2=0.802$, $df=22$, $t=9.44$, $p<0.01$; offal $r^2=0.704$, $df=18$, $t=6.539$, $p<0.01$). While fulmars consumed virtually all offal (94%) in situations where they outnumbered other species, their success declined to 33% when equal numbers of ‘‘other scavengers’’ were present (Table 9). When fulmars were in the minority, even if hundreds of these birds were present, only small amounts of offal were consumed (8%). With roundfish discards, a very similar pattern was found, in which 61% of all roundfish was taken by fulmars if these birds were numerically dominant, 22% if equal numbers of other scavengers occurred and only 5% if fulmars formed a

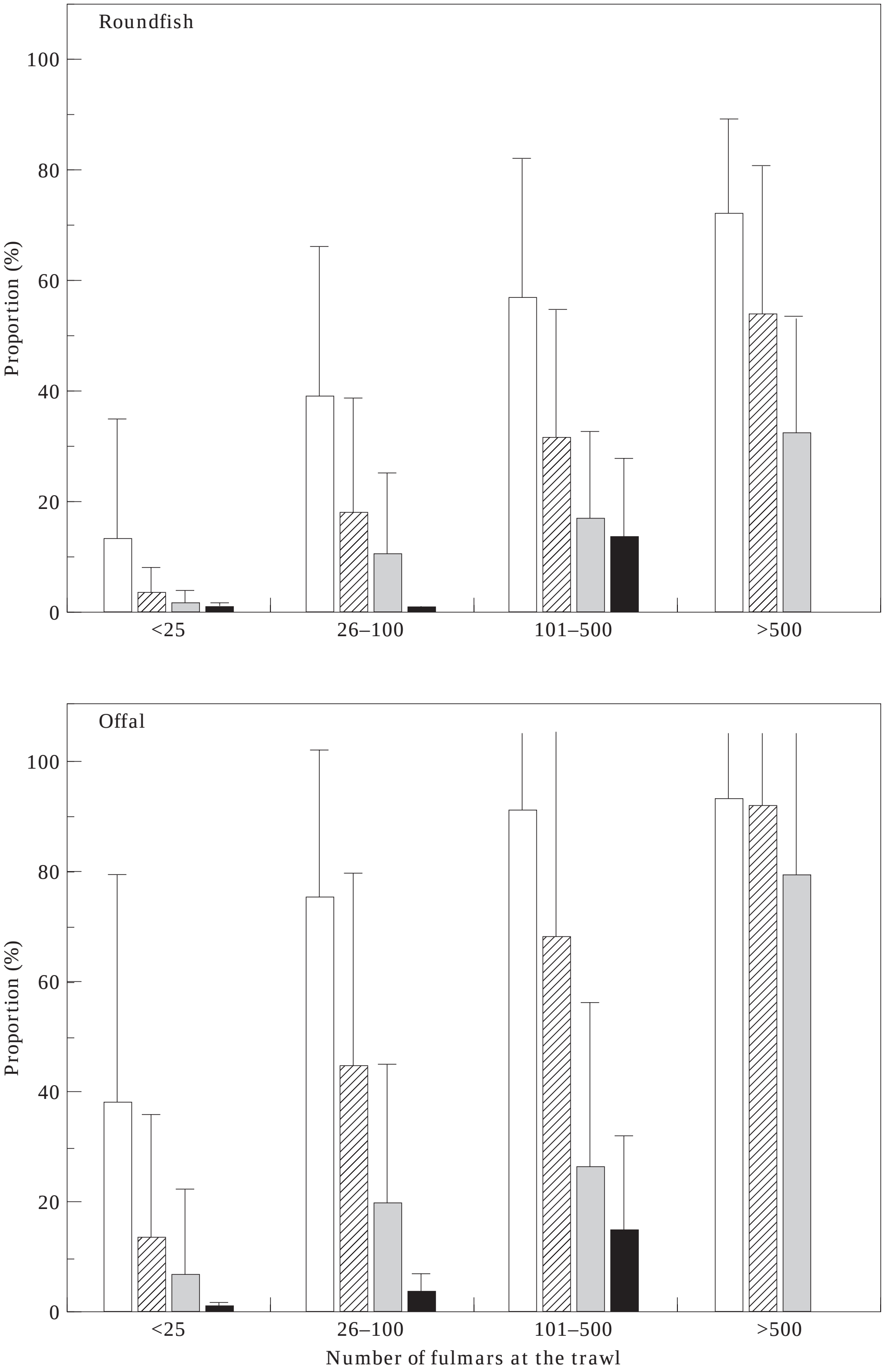


Figure 8. Roundfish (top) and offal (lower) consumption (%) by fulmars in small, medium, large and very large flocks, with variable numbers of others scavengers at the trawl. Median consumption and standard deviations are shown. Other scavengers: □ <25; ▨ 26–100; ▢ 101–500; ■ >500.

Table 9. Offal and roundfish discards consumption (%) by fulmars during experimental discarding in relation to the dominance of fulmars at the trawl. Results are presented for situations in which fulmars formed a minority (minor), occurred in equal numbers with other scavengers (equal), or were numerically dominant (domin). Overall offal and discards consumption by fulmars is given separately; — = insufficient sample or no data.

	Offal consumption			Roundfish consumption			Overall consumption	
	Minor	Equal	Dominance	Minor	Equal	Dominance	Offal	Roundfish
NW	22	30	91	11	27	52	73	34
NE	4	22	98	3	12	79	79	50
CW	5	13	98	6	13	37	78	23
C	19	56	93	5	29	76	70	39
CE	5	—	83	2	11	94	5	18
S	1	74	—	2	5	—	10	2
Spring	7	44	94	13	29	63	34	39
Summer	12	62	98	4	19	65	82	43
Autumn	5	14	61	1	9	38	14	6
Winter	11	56	77	0	3	5	52	1
Totals	8	33	94	5	22	61	59	30

minority (Table 9). Moreover, fulmars dropped or otherwise lost 36% of all roundfish handled when they dominated at the trawl, but over 65% when equal or larger numbers of other scavengers occurred. These results suggest that fulmars were easily outcompeted by other scavengers, particularly so with regard to roundfish.

Hence, the probability that a fulmar consumed roundfish discards or offal during sessions of experimental discarding was positively related to the relative abundance of fulmars at the trawl. With roundfish discards, fulmars consumed considerably less than expected on the basis of their numbers at the trawl (Fig. 9), whereas offal was obtained in accordance with their numerical abundance (Fig. 10). The effect of regions and seasons contributed significantly to the logit model that was assumed for the analysis of the relation between discards consumption by fulmars and their relative abundance at trawls (Tables 10 and 11). Contrary to what might be expected from the earlier analysis, absolute numbers of ‘‘other scavengers’’ at a trawl did not greatly influence the probability that a fulmar consumed a given roundfish (Table 10). Hence, ten fulmars in a flock with ten other scavengers did not perform better or worse than 100 fulmars in a flock with 100 other scavengers.The probability, p, of roundfish discard consumption by fulmars was particularly low in autumn and winter and also in regions NW and CW (Fig. 11). For offal consumption, this probability was particularly low in autumn and in CW, whereas fulmars in summer consumed considerably more of the discarded offal than their relative abundance at trawls would have predicted.

Feeding success at fishing vessels

The foregoing results suggest that fulmars, in terms of overall discards consumption, performed better in situations where they were numerically dominant at the trawl. In situations where such flocks were most common (regions NW, NE, CW and C in spring and summer, and region NE in autumn; Table 8), fulmars consumed 85% of all discarded offal items (n = 4675) and 43% of all roundfish (n = 20 837). Elsewhere in the North Sea and in other seasons, offal consumption by fulmars was only 19% (n = 3094) and roundfish consumption no more than 11% (n = 13 785). A distinct decrease in overall consumption rate of roundfish and offal was recorded in autumn and winter (Fig. 12; Table 9). In these surveys, fulmars were relatively less important consumers of fishery waste, with kittiwakes and, particularly, herring gulls achieving higher status than in summer (Camphuysen *et al.*, 1995).

The importance of offal and discards in fulmar diets

Small amounts only of benthic invertebrates and flatfish were taken by fulmars. Consumption of roundfish discards and offal, however, was quite important. Using the length distribution of roundfish selected from the discards fraction, the proportion of the total mass of roundfish discards taken by fulmars was calculated (region NW 32%, NE 39%, CW 20%, C 44%, CE 5%, S 3%). Secondly, the proportion of offal items offered that were taken by fulmars was used as an estimate of the proportion of the total mass discharged in commercial fisheries (NW 73%, NE 78%, CW 72%, C 60%, CE 6%, S 7%). We assumed an energetic value of roundfish of 5 kJ g^{-1} and of offal of 9 kJ g^{-1}, an assimilation efficiency of 75%, and a conservative estimate of the energetic requirements of fulmars of 13W (FMR = 2.5 × BMR; Bryant and Furness, 1995; Hunt and Furness, 1996). Using estimates of discarded quantities of

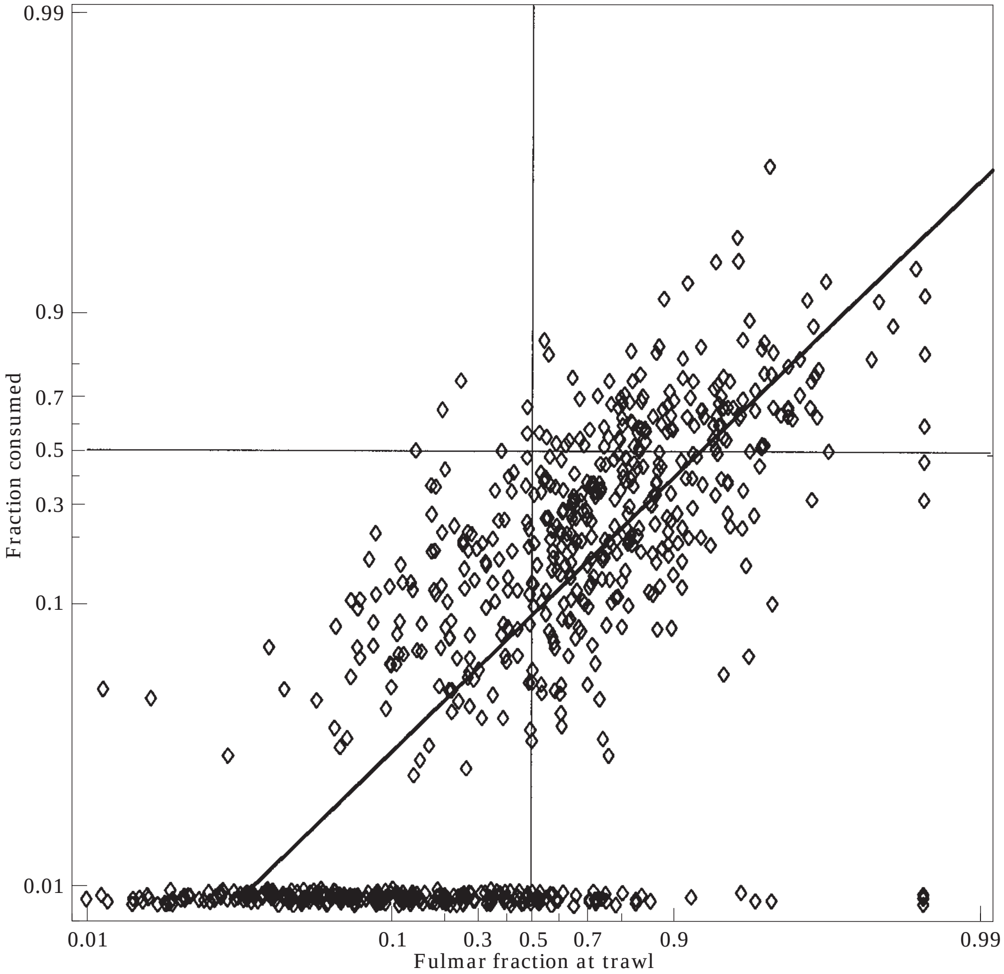


Figure 9. Relationship between the relative abundance of fulmars at the trawl (proportion of all scavengers) and roundfish consumption (proportion of consumed roundfish taken by fulmars). Scales according to logit transformation. Data are from 749 experiments.

discards and offal per region from Garthe *et al.* (1996), and mean estimates of total numbers of fulmars at sea in each of the regions, we find that in regions NE, CW, and C, approximately 70% of the energetic requirements of the fulmars were met by discards and offal (Fig. 13). In NW, CE and S, less than one third of the fulmars at sea were sustained by fishery waste. Applying this calculation to the respective seasons, while assuming ‘‘constant’’ fishing effort (Furness *et al.*, 1992), it is clear that discards and offal are of great significance in spring and summer, but relatively unimportant food sources for fulmars in autumn and winter (Fig. 14). Overall, we estimate that discards and offal fulfilled ca. 48% of the energetic needs of fulmars in the North Sea.

Discussion

From the analysis of fulmar and fisheries distribution, it is obvious that the birds do not necessarily move to areas where most trawlers can be expected, nor to areas where the largest amounts of discards (tonnes per km^{-2}) are produced. On a North Sea scale and throughout the year, fulmars must be considered northerly, pelagic seabirds that generally avoid the coastal waters of the German Bight and the Southern Bight.

Hudson and Furness (1988) concluded that fulmars at fishing boats around Shetland obtained virtually all the offal produced and offered, but very few discarded fish (2%). This study, however, showed that, on average, 30% of all discarded roundfish is consumed by fulmars and that up to 90% of certain (small) fish species may be taken. Fulmars are rather ill-adapted as scavengers, particularly around trawlers that travel while fish are sorted and discarded. Being stiff-winged and not very manoeuvrable in flight is a serious disadvantage in competitive situations with gulls. Their poor diving ability is also a disadvantage when competing with gannets. Dense flocks of fighting individuals effectively

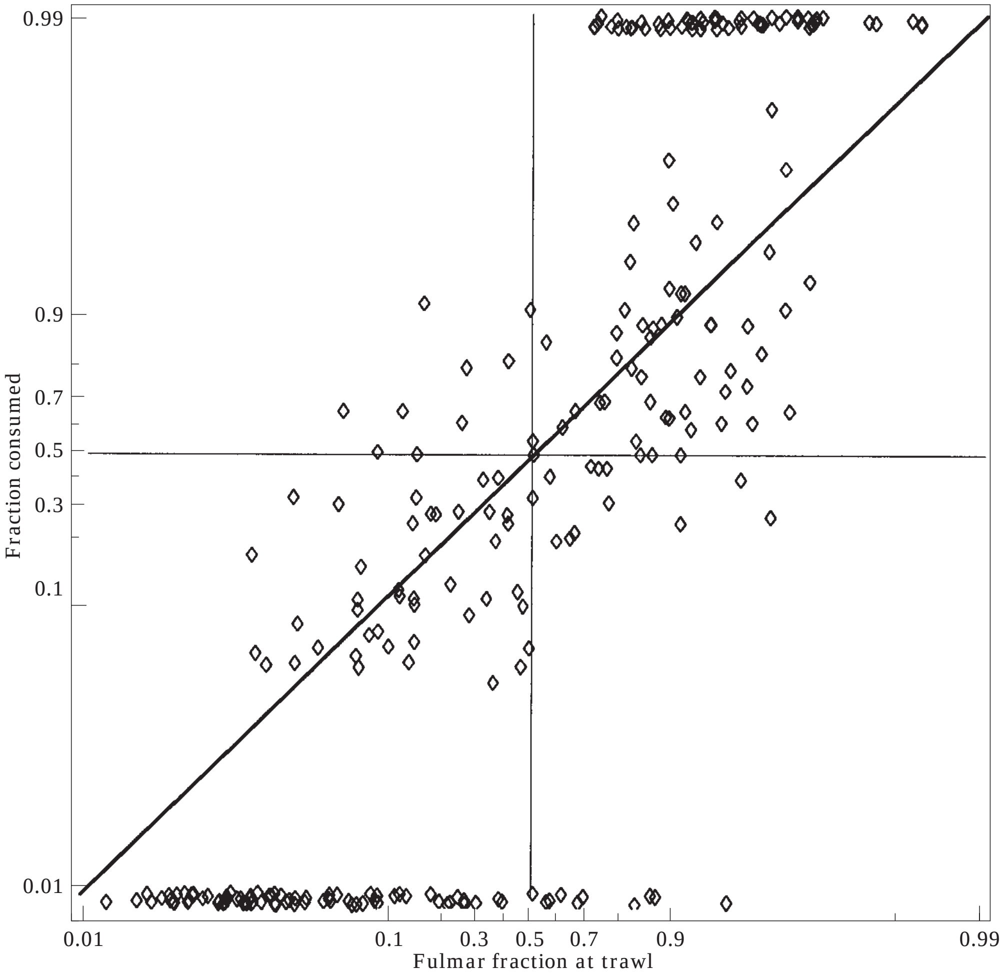


Figure 10. Relationship between the relative abundance of fulmars at the trawl (proportion of all scavengers) and offal consumption (proportion of consumed offal taken by fulmars). Scales according to logit transformation. Data are from 254 experiments.

Table 10. Degrees of freedom (df), deviance and mean deviance of various logit models (in increasing order of complexity) that relate the probability of consumption of roundfish discards by fulmars to the effects of total numbers of other scavengers, region, season or a combination of these factors (n=723 experiments in which roundfish were offered). See Methods for further explanation.

Model	df	Deviance	Mean deviance
Null model ($a=1$, $b=1$)	723	15 452	21.37
$b=1$	722	7 453	10.32
Basic model	721	7 426	10.30
+region+season ($b=1$)	714	5 609	7.86
+region+season	713	5 510	7.73

Table 11. Degrees of freedom (df), deviance and mean deviance of various logit models (in increasing order of complexity) that relate the probability of consumption of offal by fulmars to the effects of total numbers of other scavengers, regions, season or a combination of these factors (n=245 experiments in which offal was offered). See Methods section for further explanation.

Model	df	Deviance	Mean deviance
Null model ($a=1$, $b=1$)	245	1406	5.739
$b=1$	244	1403	5.751
Basic model	243	1251	5.150
+region+season ($b=1$)	236	833	3.528
region+season	235	832	3.539

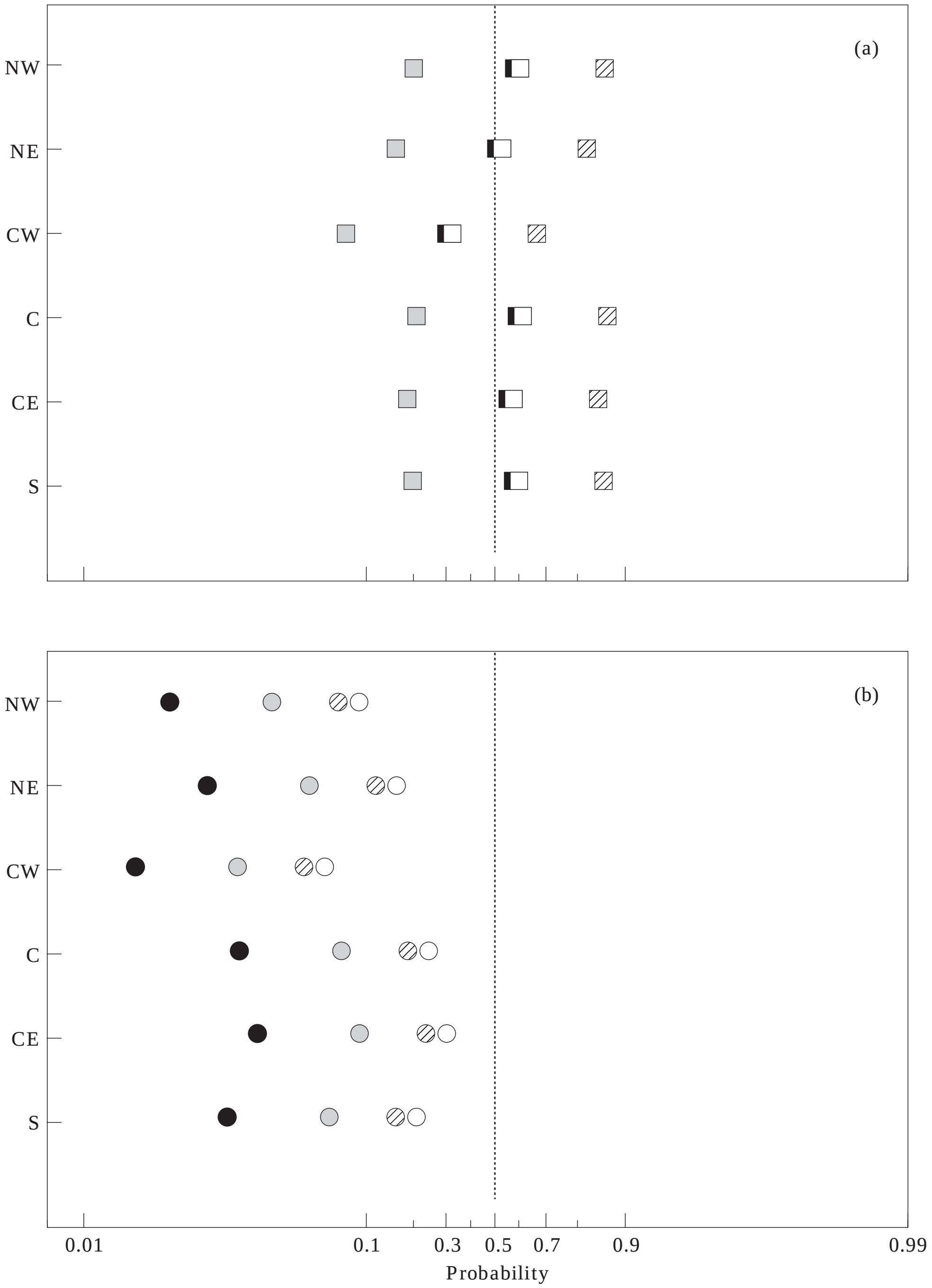


Figure 11. Probability of (a) offal and (b) roundfish consumption by a fulmar in six regions and four seasons (see text). □○ spring; ▨⊘ summer; ⊡◍ autumn; ■● winter.

excluded all but the most powerful kleptoparasites and only great black-backed gulls and gannets could reach discards under these conditions. In winter, the manoeuvrable kittiwakes appeared to be more efficient consumers of offal than fulmars, and only in summer, when kittiwakes were not present in very large numbers at fishing vessels (Camphuysen, 1995), were fulmars the most important consumers of offal.

This study showed that fulmar attendance at trawlers in autumn and winter was very much reduced. They appeared quite suddenly to stop forming scavenging groups in which they are numerically dominant, and

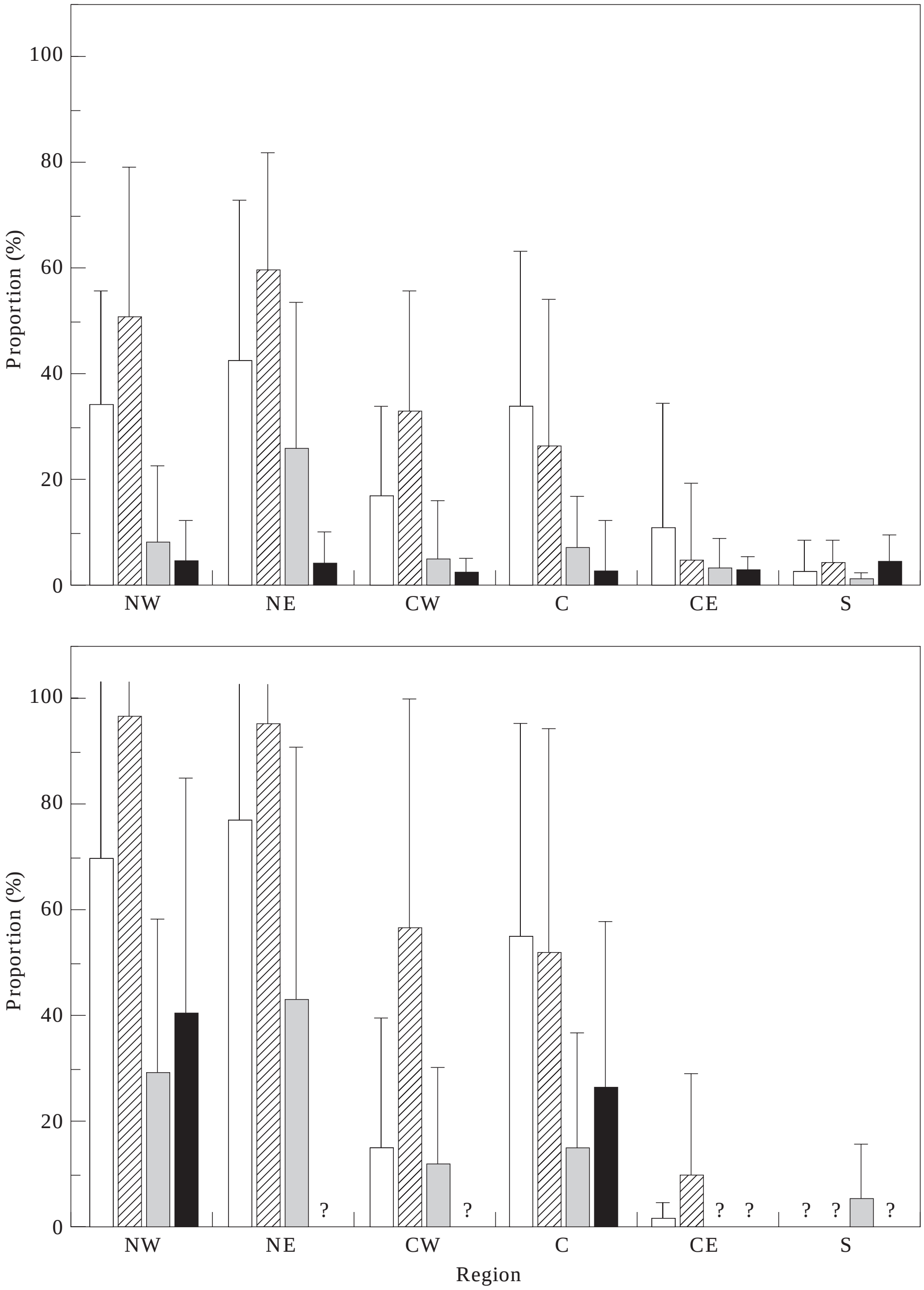


Figure 12. Roundfish (top) and offal (lower) consumption (%) by fulmars in each region in spring, summer, autumn and winter. Median consumption and standard deviations are shown. ? indicates no data. □ spring; ▨ summer; ░ autumn; ■ winter.

their overall feeding success also declined markedly. The total number of fulmars in the North Sea peak in summer and gradually decline in autumn to winter, but such a sudden decline in foraging success is difficult to explain. However, considering that fulmars are highly vulnerable to kleptoparasitism, particularly when exploiting roundfish, it may result from a change in the relative abundance of other scavengers. Camphuysen *et al.* (1995) demonstrated that herring gulls suddenly become very abundant scavengers at fishing vessels all over the North Sea, including offshore waters in the north that are dominated by fulmars in spring and summer. It is possible that the increase of competitors at trawlers, particularly of herring gulls (Camphuysen

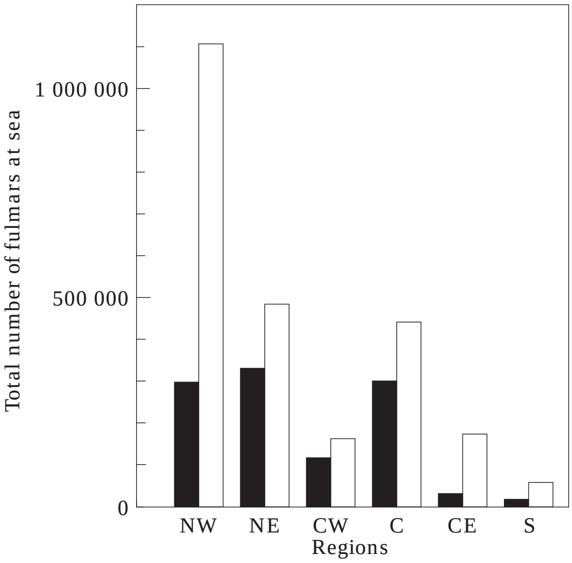


Figure 13. Mean total number of fulmars at sea in each region (open bars) and the number of birds potentially sustained by offal and roundfish discards (black bars) (see text).

et al., 1995; Stone *et al.*, 1995), leads to reduced foraging success of scavenging fulmars.

Although one of the most vulnerable species to kleptoparasitism, fulmars are highly successful scavengers at trawlers in the northern North Sea, where they outnumber all other species and, apparently, obtain substantial proportions of their food from commercial fisheries. However, fulmars are known to have an extremely varied diet, which includes fish, zooplankton, squid and carrion (Cramp and Simmons, 1977; Camphuysen, 1990). Their preference for certain water types in the North Sea that resemble clear, saline Atlantic waters (which historically may be considered their more natural habitat; Fisher, 1952), indicates that the availability of their natural prey may play an important role in their pelagic distribution. Future studies are essential in order to identify the ‘‘natural foods’’ in these areas in different seasons. In such waters, occasional trawlers attract vast numbers of fulmars and the birds appear reluctant to leave these hydrographical conditions to enter coastal regions with large fisheries in the southeastern half of the North Sea. The occurrence of large numbers of fulmars here is unpredictable and invasive in character (Camphuysen and Van Dijk, 1983; Camphuysen, 1989; Camphuysen and Leopold, 1994). Midsummer wrecks in hot summers, when large numbers of dead and moribund birds are washed ashore, and influxes associated with violent storms in autumn and winter, result in larger than usual numbers of fulmars in areas that they normally avoid.

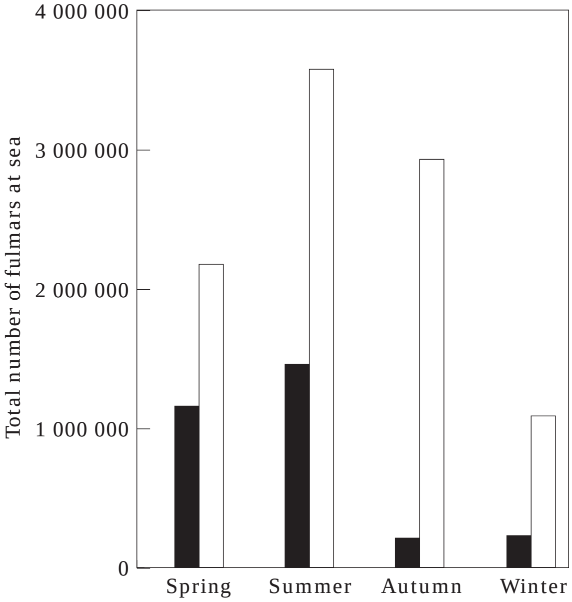


Figure 14. Mean total number of fulmars at sea in each season (open bars) and the number of birds potentially sustained by offal and roundfish discards (black bars), assuming ‘‘constant’’ fishing effort over the year (see text).

This study estimated that less than 50% of the energetic requirements of fulmars may be satisfied by offal and roundfish discards. Considering also the clear relationship between fulmar numbers and specific hydrographical features, this highlights the need for more detailed study of fulmar diet and prey selection. To date, most information on fulmar diet has been obtained from studies at breeding colonies. Field studies are now urgently required to unravel the feeding strategies of North Sea fulmars outside the breeding season and at sea.

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