HERRING GULL *Larus argentatus* AND LESSER BLACK-BACKED GULL *L. fuscus* FEEDING AT FISHING VESSELS IN THE BREEDING SEASON: COMPETITIVE SCAVENGING VERSUS EFFICIENT FLYING

KEES (C.J.) CAMPHUYSEN

ABSTRACT The distribution and feeding range of Herring Gulls and Lesser Black-backed Gulls breeding on the Dutch Wadden Sea islands were assessed, using the results of ship-based surveys in the southern North Sea. The occurrence of both species in association with commercial fishing vessels is decribed in relation to distance to the coast and distance to the colonies. The feeding range of Lesser Black-backed Gulls (95% of all birds within 135 km of the colony) was considerably larger than that of Herring Gulls (95% within 54 km), and this difference could not be explained by differences in flight capacities. Feeding success and vulnerability to robbery of both species as scavengers at fishing vessels are described. Neither the vulnerability to robbery indices, nor the feeding success indices of both species did support earlier suggestions that Lesser Black-backed Gulls may have outcompeted Herring Gulls at (nearshore) fishing vessels. The feeding range of Lesser Black-backed Gulls could not solely be explained by a general avoidance of Herring Gulls near the coast, nor by the presence fishing vessels further offshore in comparison with the coastal zone. It is concluded that the large feeding range was motivated by a third, but unknown factor. The reduction of fisheries near the coast has probably led to a reduction in feeding opportunities for scavengers near the coast.

Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands.

INTRODUCTION

Breeding numbers of Herring Gulls *Larus argentatus* on Terschelling (one of the major gull colonies in the Netherlands) increased from 6-8000 pairs in the late 1960s to just over 21,000 pairs in 1982-83, but subsequently declined to less than 15,000 pairs in 1992 and 1993 as a result of poor breeding success (Noordhuis & Spaans 1992, Van Dijk *et al.* 1994, Koks 1994). Lesser Black-backed Gulls *L. fuscus* in the same colony increased from a few hundreds in the late 1960s to 13,000 pairs in 1985 (68% of the total Dutch population) and subsequently stabilised on some 11,500-13,350 pairs in 1992 and 1993 (Van Dijk *et al.* 1994, Koks 1994). Hence, the ratio between numbers of gulls breeding on Terschelling has changed in favour of the latter species. Lesser Black-backed Gulls primarily feed on marine fish (Noordhuis 1987), whereas the diet of Herring Gulls is more diverse and includes many kinds of (marine) fish, marine invertebrates, terrestrial animals, carrion and refuse, grain and berries (Spaans 1971). During 1985-1987, the occurrence of marine fish in the diet of Herring Gulls amounted to only 14% of levels found in 1966-68 (Noordhuis 1987, Spaans & Noordhuis 1989).

The diet of both Herring and Lesser Black-backed Gulls includes several demersal fish species which cannot normally be caught by plunge diving, but which commonly occur in the bycatch of beamtrawlers. It was therefore concluded that part of the fish brought ashore by these gulls was obtained at fishing vessels in the North Sea. The increase in numbers of breeding Lesser Black-backed Gulls on Terschelling was assumed to

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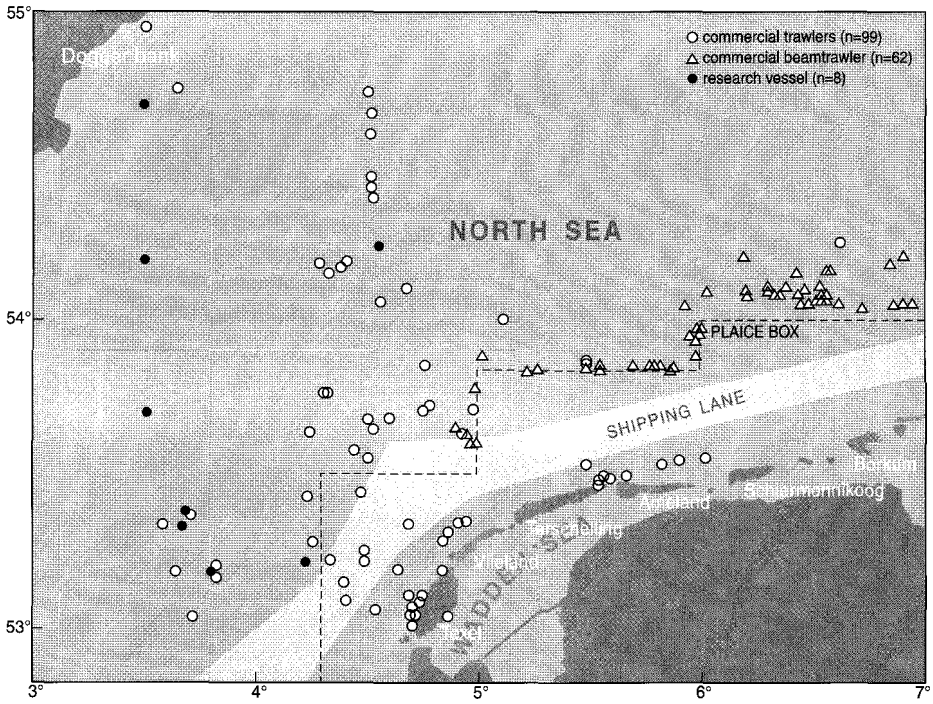

Fig.1. Counts of groups of scavenging seabirds at commercial fishing vessels and research vessels in the southern North Sea in summer (May-August, 1987-1993, n = 169 counts). Shown are the outer borders of shipping lane north of the Wadden Sea islands and the plaice-box (dotted lines; see text). Plots include counts of seabirds onboard fisheries research vessels (n = 8), onboard a commercial beamtrawler (n = 62), counts of associated birds at nearby, actively fishing commercial fishing vessels during ship-based surveys at sea (n = 67) and birds associated with commercial fishing vessels as recorded from the shore (n = 32).

have forced Herring Gulls to concentrate more on other food resources than before (Noordhuis & Spaans 1992). This change in feeding habits of the Herring Gull and the increased intra-specific competition were hypothesized to have contributed to the decline in breeding success which has taken place compared to the late 1960s (Spaans & Noordhuis 1989). Studies in West Scotland indicated, however, that Lesser Black-backed Gulls were approximately two times more successful than Herring Gulls as scavengers behind fishing vessels (Furness *et al.* 1988). In this paper an analysis of sightings of scavenging gulls at fishing vessels is presented, with special emphasis on feeding areas during the breeding season and around the breeding colonies, particularly off Terschelling. Results of experimental discarding of fish from a commercial beamtrawler in summer 1993 were analysed to obtain information on interspecific competition of these gulls at fishing vessels in the area. The analysis was meant to investigate whether the suggestion that interspecific competition between Lesser Black-backed and Herring Gulls at fishing vessels may have forced the Herring Gulls towards exploiting other sources of food could be supported.

STUDY AREA AND METHODS

Study area

The area under study in this analysis was bor-

dered by 53°-55°N latitude, and 3°-7°E longitude (Fig. 1), including the coastal zone of all Dutch Wadden Sea islands up to the Dogger Bank in the northwest. Shown in Fig. 1 are a system of *shipping lanes* off the Wadden Sea islands, which runs roughly from west to east and in which most shipping traffic is concentrated and the position of a *plaice-box*, established in the late 1980s to protect immature flatfish. Within the shipping lanes, fishing is not prohibited, but the area is unattractive to fishermen because of heavy traffic in a relatively narrow strip and because of specific traffic regulations which also apply to fishing vessels. Large beamtrawlers (>300 Hp) are not allowed to fish within 12 miles (*c.* 22 km) from land and heavy beamtrawlers are not allowed to use the Plaice-box in summer. Approximately between 53°30'N, 4°E and 54°N, 5°E, the Frisian Front area is located, an enriched zone which attracts piscivorous seabirds and fisheries (Leopold 1991).

At sea distribution

Since 1987, the distribution of seabirds in the southern North Sea has been studied by means of ship-based surveys, organised by the Netherlands Institute for Sea Research (NIOZ), the Dutch Seabird Group (NZG)/Tidal Waters Division of the Ministry of Transport, Public Works and Water Management (DGW) and the Institute for Forestry and Nature Research (IBN-DLO). Seabirds were counted during steaming in a strip-transect aside the ship (used to assess numbers per km^2) and in a 180° scan ahead of the ship (used to assess numbers per km travelled; *cf.* Tasker *et al.* 1984). During these surveys, fishing vessels were recorded when any seabirds were associated and all birds in these flocks were identified and counted (Camphuysen 1993a). In 1992 and 1993, additional information on the occurrence of scavenging seabirds was collected by means of observations of inshore commercial fishing vessels from coastal sites, during fishing onboard fishery research vessels, and onboard a commercial beamtrawler. For each count of seabirds attending a trawler during May-August, the distance to the nearest coast and the nearest (large) colony was calculated. Coastal colonies of Herring Gulls and Lesser Black-backed Gulls occur on most Wadden Sea islands (Table 1) and scattered along the mainland coast. In order to estimate feeding ranges during the breeding season, the distance to the nearest colony and the presence of adult Herring and Lesser Black-backed Gulls were assessed for

Table 1. Breeding numbers (pairs) and number of colonies of Herring Gulls and Lesser Black-backed Gulls on the Dutch Wadden Sea islands in 1993 (Koks 1994), and geographical positions of colonies used for feeding range calculations.

		Herring Gull		Lesser Black-backed Gull	
Subregion		Colonies	Pairs	Colonies	Pairs
Waddensea islands		9	40644	8	19398
Rottumeroog	(53°32.5'N, 6°35.0'E)		3256		145
Rottumerplaat	(53°32.5'N, 6°27.0'E)		2525		115
Schiermonnikoog	(53°30.0'N, 6°16.0'E)		4295		4295
Ameland	(53°27.5'N, 5°53.0'E)		2609		109
Terschelling	(53°26.0'N, 5°27.0'E)		14860		13350
Vlieland	(53°17.0'N, 4°59.0'E)		9907		1007
Texel, De Geul	(53°0.0'N, 4°43.5'E)				
Texel, De Muy	(53°8.0'N, 4°47.5'E)		3162		377
Griend			30		-

each count of seabirds attending a trawler and for each 10-minute count during ship-based strip-transect counts at sea in summer (May-August 1987-1993). Densities at sea of Herring Gulls and Lesser Black-backed Gulls (around Terschelling only) in relation to the nearest colony were modelled. Densities were calculated in radial strata of 1 km width around colonies. The relative abundance of adults of these gulls at sea (n/km^2) with increasing distance to the colony were modelled, assuming that counts were Poisson-like-distributed by calculating the expected mean density as a function $\mu = \mu_0.e^{-a.distance}$ of the distance, obtained by maximising the likelihood. Dimensions needed for flight calculations were taken from adult gulls found dead on Texel and from literature. BASIC programmes were used to calculate fuel consumption in relation to distance of flight for both Herring and Lesser Black-backed Gulls (Prog_1a in Pennycuick 1989).

Experimental discarding

Fishery waste comprises offal (waste from gutted, marketable fish), undersized roundfish, undersized flatfish, damaged marketable fish and benthic invertebrates. Onboard a commercial 2000 Hp beamtrawler in June-August 1993, samples of fish, offal and invertebrates were taken from the discards fraction of the catch. The items were identified, total lengths of fish were measured to the nearest cm, and discarded into the sea while the catch was sorted and gutted (thrown into to the steady trickle of discards produced by the ship's crew). Attempts by seabirds to pick up and swallow items were recorded into a tape recorder, noting the species and age class of the bird taking the item, whether the item was eaten, dropped or stolen. If it was stolen, the same notes were made for the second and subsequent birds, until the item was finally lost (sunk) or swallowed. During these discarding experiments the numbers and age classes of scavenging seabirds of each species were recorded so that fish consumption could be related to scavenging flock composition (*cf.* Hudson & Furness 1988, Camphuysen *et al.* 1993, Camphuysen 1993b). Feeding success of scavenging Herring Gulls and Lesser Black-backed Gulls at the trawl were compared, also in relation to other scavengers commonly occurring at the trawl (Fulmar *Fulmarus glacialis*, Great Black-backed Gull *Larus marinus* and Kittiwake *Rissa tridactyla*), and feeding strategies were described. Frequencies of robbing of experimentally discarded items by one bird from another were assessed, in order to evaluate the dominance hierarchies at the trawler. A '*vulnerability to robbery index*' (number of experimental discards stolen from a species divided by the number of experimental discards stolen by that species) was calculated for all species commonly occurring at the trawler. Feeding '*success rates*' of scavengers are defined as the proportion of discarded items of a particular type that are consumed by a species, divided by the proportion of all scavenging birds at the vessel of that species. Thus, if all seabirds are equally successful in obtaining discards the success index will be 1.0 for each species. A success index greater than 1.0 indicates that the species in question obtained a greater proportion of the discards than expected from the numbers present. The number of discards expected to be eaten was calculated (on the basis of the numerical abundances of each scavenging seabird species) and compared with observed numbers using a χ^2-test (with the null hypothesis of equal success for all species).

OBSERVATIONS

Herring Gulls and Lesser Black-backed Gulls at sea

Herring Gulls were mainly restricted to the zone of 25 km from the nearest shore (Fig. 2, Table 2). Densities (*n*/km^2) of adults during ship-based strip-transect counts declined with a rate of 8.2% per km away from the coast within the study area from a mean density of 1.74/km^2 within 1 km from the coast (Poisson regression; $y = 1.735 \cdot e^{(0.082 \cdot dcst)}$; where dcst= distance to the nearest coast in km). Beyond the shipping lanes, Herring Gulls were quite rare during most of the summer.

Table 2. Observer effort (number of 10-minute counts and km travelled), relative abundance of Herring Gulls and Lesser Black-backed Gulls at sea (*n*/100km), and the proportion of adults (%; sample size in parentheses) in six distance zones to the nearest coast, May-Aug 1987-93, 53-55°N, 03-07°E.

Distance zone	Number of counts	Distance travelled (km)	Herring Gull		Lesser Black-backed Gull	
			n/100km	% adult (*n*)	*n*/100km	% adult (*n*)
0-5 km	701	1710	228.7	88.8 % (1843)	229.5	89.9 % (1974)
5-10 km	370	988	107.0	91.8 % (485)	220.6	89.1 % (1047)
10-25 km	499	1614	37.2	83.1 % (260)	95.5	90.3 % (1610)
25-50 km	859	2768	10.4	78.9 % (71)	85.2	93.4 % (1370)
50-100 km	1362	4624	1.9	93.7 % (861)	35.4	92.5 % (1273)
>100 km	1141	4356	0.5	33.3 % (15)	3.4	57.1 % (98)

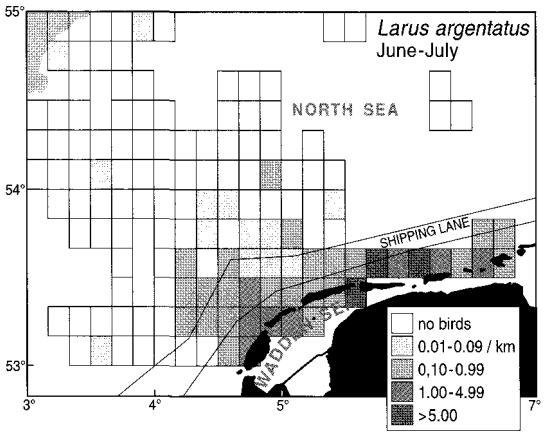

Fig. 2. Distribution of Herring Gulls at sea (number per kilometre travelled) during chick rearing, June-July 1987-1993 (modified after Camphuysen & Leopold 1994).

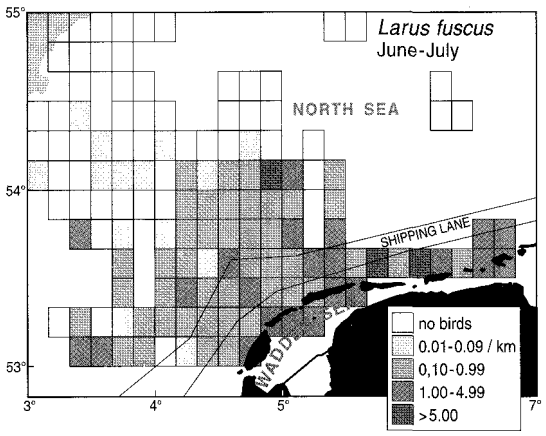

Fig.3. Distribution of Lesser Black-backed Gulls at sea (number per kilometre travelled) during chick rearing, June-July 1987-1993 (modified after Camphuysen & Leopold 1994).

Adult gulls predominated in most areas, but immatures were relatively numerous at over 100 km from the coast (Table 2). Comparatively large numbers were seen at over 50 km from the shore to the northwest of Texel and Vlieland, an area rich in offshore installations (Placid Field and associated installations). Large gulls are known to roost on oil and gas platforms in considerable numbers during most of the year (Tasker *et al.* 1986), but those associated with offshore installations during the breeding season are probably non-breeding birds.

Lesser Black-backed Gulls were more widespread and occurred also in large numbers at substantial distances from the coast (Fig. 3, Table 2). Densities (*n*/km^2) of adult Lesser Black-backed Gulls during ship-based strip-transect counts declined at a rate of 2.9% per km away from the coast from a mean density of 1.74/km^2 within 1 km from the coast (Poisson regression; $y = 1.737 \cdot$

Table 3. Relative abundance (number per 100 km travelled) of commercial fishing vessels in six distance zones to the nearest coast, from ship-based surveys, May-Aug 1987-93, 53-55°N, 03-07°E.

Distance zone	km travelled	fishing vessels Number	*n*/100km
0-5 km	1710	13	0.8
5-10 km	988	5	0.5
10-25 km	1614	6	0.4
25-50 km	2768	15	0.5
50-100 km	4624	16	0.3
>100 km	4356	12	0.3

$e^{(0.029 \cdot dcst))}$. In contrast to Herring Gulls, this species occurred frequently beyond the shipping lanes and in the Frisian Front area. Around 90% of all Lesser Black-backed Gulls were adults, except at great distances from the coast (Table 2).

Herring Gulls and Lesser Black-backed Gulls at fishing vessels

Commercial fishing vessels were widespread, but occurred in relatively high numbers within 5 km from the nearest coast and just around the edge of the plaice-box. The lowest number of fishing vessels observed per km travelled were found at >100 km from the coast (0.28/100km travelled; Table 3). Within 5 km from the shore, the chance of spotting a fishing trawler was 2.7x higher (0.76/100km). Herring Gulls were particularly abundant at inshore fishing vessels, with small numbers occurring in flocks of scavengers beyond the shipping lanes (Fig. 4). Of 81 records of Herring Gulls at fishing vessels, 17 records were of groups of over 100 individuals (21%). Of these, 16 occurred within 4 km from the nearest coast, one group was found at 7 km from the coast. Groups of >10 Herring Gulls were also clearly concentrated near the shore (80% within 10

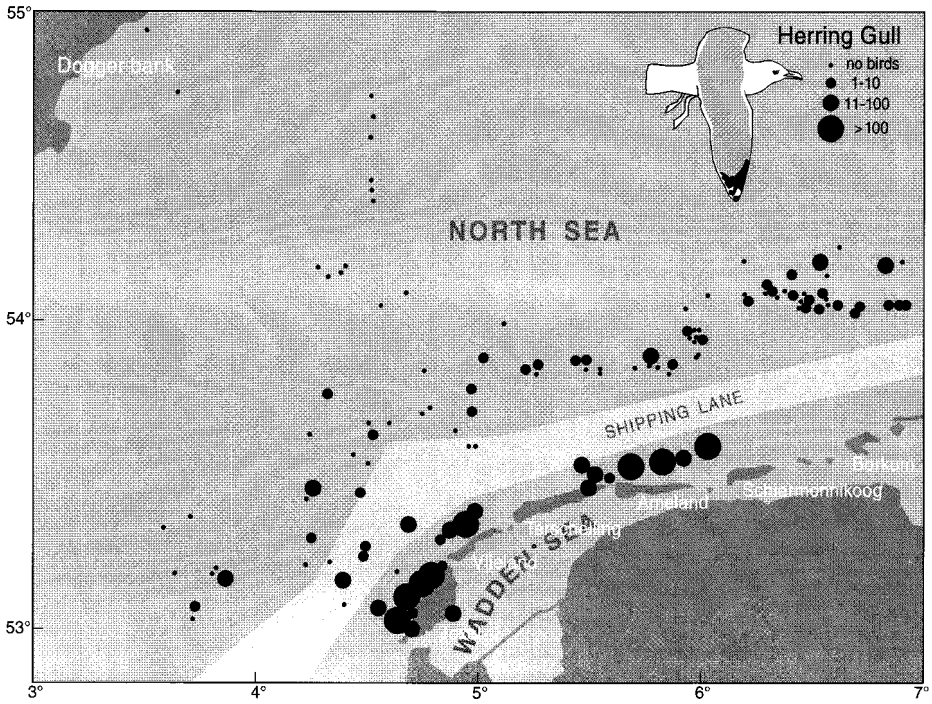

Fig.4. Abundance of Herring Gulls at fishing vessels off the Dutch Waddensea islands, May-August 1987-1993 (n = 81 records). Counts of associated seabirds at fishing vessels where Herring Gulls were not positively identified are indicated by small dots.

Table 4. Observed and expected frequencies of occurrence of ≥10 Herring Gulls or Lesser Black-backed Gulls in flocks of scavenging seabirds attending fishing vessels and proportion of adults (%; sample size in parentheses) in six distance zones to the nearest coast, May-Aug 1987-93, 53-55°N, 03-07°E. Stern counts include sightings of commercial fishing vessels during ship-based surveys and from the coast, counts at the stern of fishing research vessels and counts onboard a commercial beamtrawler (see figure 1). Expected frequencies are based on total number of counts at fishing vessels in each zone, within 100 km from the coast. The null-hypothesis of equal distribution of fishing vessels and groups of >10 gulls in this area was tested (χ^2-test).

Distance zone	all stern counts	Herring Gull			Lesser Black-backed Gull		
		obs.	exp.	% adult (*n*)	obs.	exp.	% adult (*n*)
0-5 km	45	27	11.8	93.7 % (3590)	16	27.1	99.6 % (268)
5-10 km	5	5	1.3	98.3 % (119)	3	3.0	99.2 % (260)
10-25 km	6	3	1.6	90.0 % (10)	4	3.6	72.7 % (11)
25-50 km	51	2	13.3	93.6 % (79)	37	30.7	94.2 % (8526)
50-100 km	46	3	12.0	93.0 % (43)	32	27.7	94.6 % (6657)
>100 km	16	0	0				
Total (<100 km)	153	40	40	93.8 % (3841)	92	92	94.6 % (15722)
χ^2		22.1			3.6		
df		4			4		
p		$p < 0.001$			n.s.		

km from the coast, $n = 40$; Table 4). Observed frequencies of occurrence of such groups in five distance zones off the coast were significantly different from expected frequencies, based on total number of counts at fishing vessels in each zone (χ^2 22.1, df = 4, $p < 0.001$). The largest concentration of Herring Gulls at a trawler were 800 individuals associated with a shrimper off Texel (21 June 1993). Adults predominated in all zones (93.8%, $n = 3841$; Table 4).

Small numbers of Lesser Black-backed Gulls occurred at fishing vessels near the shore, but large groups were seen scavenging at fishing vessels in the vicinity of the major colonies at Texel and Terschelling (Fig. 5). Numbers of Lesser Black-backed Gulls in association with offshore fishing vessels were usually larger, often including several hundreds of birds in a single count. Observed frequencies of occurrence of groups of ≥10 Lesser Black-backed Gulls at fishing boats were not significantly different from expected frequencies, based on total number of counts at fishing vessels in each zone ($\chi^2 = 3.6$, df = 4, n.s.; Table 4). The largest concentration of Lesser Black-backed Gulls at a trawler comprised 1060 individuals at only 2 km from the shore (8 July 1987, unidentified trawler, off Ameland). In all areas, adults predominated (94.6%, n = 15 722; Table 4).

Distance to nearest colony

Modelling the densities of adult Herring Gulls at sea in 1 km strata around the nearest colonies resulted in similar patterns as described for densities with increasing distance to the nearest coast ($y = 2.591 \cdot e^{(-0.086 \cdot dcol)}$; where d_{col}= distance to the nearest colony in km). Around Terschelling, distance to the coast was of greater importance than distance to the colony, as can be concluded from a decline of 8.4% per km away from the colony perpendicular to the coast and 0.4% per km away from the colony along the coast ($y = 2.07 \cdot e^{(-(0.004 \cdot dcol) - (0.084 \cdot dcst))}$). The largest colony of Lesser Black-backed Gulls within the study area is found on Terschelling (nearly 70% of the Wadden Sea breeding population of 16,600 pairs in

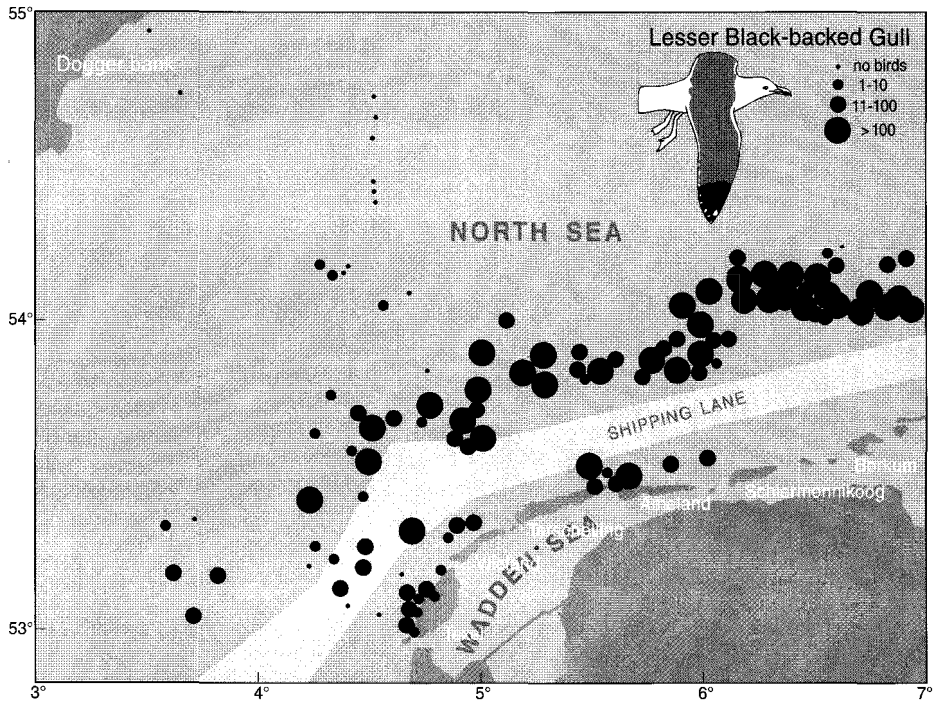

Fig.5. Abundance of Lesser Black-backed Gulls at fishing vessels off the Dutch Wadden Sea islands, May-August 1987-1993 (n = 122 records). Counts of associated seabirds at fishing vessels where Lesser Black-backed Gulls were not positively identified are indicated by small dots.

1992; Van Dijk *et al.* 1994). Densities (y) at sea around Terschelling dropped gradually, from 3.7/km^2 within 2 km from the colony with a rate of 3.5% per km away from the colony perpendicular to the coast and 2.1% per km away from the colony along the coast
($y = 3.706 \cdot e^{(-(0.021 \cdot dcol) - (0.014 \cdot dcst))}$; Fig. 6).

Fuel consumption in relation to distance of flight

Lesser Black-backed Gulls are relatively longer winged than the heavier Herring Gull (Table 5). As a result, Lesser Black-backed Gulls have potentially a 13% wider feeding range than Herring Gulls, using calculations from Pennycuick (1989). In both species, differences in wing length are significant between sexes (Table 5). Therefore, female Herring Gulls have potentially a 13% longer range than conspecific males, and female Lesser Black-backed Gulls have an 11% longer range than males of the same species. The differences in fuel consumption per unit distance, however, are rather small and are even quite similar in female Herring Gulls and male Lesser Black-backed Gulls (3.80 kJ/km at maximum range speed; Table 6). Hence, the different feeding range of both species around Terschelling, as indicated by a 8.4% decline in number per km perpendicular to the coast for Herring Gulls (95% of all gulls within 54 km of the colony) and a 3.5% decline per km for Lesser Black-backed Gulls (95% of all individuals within 135 km), is difficult to explain by interspecific differences in flight performance (Fig. 7).

Feeding strategies at fishing vessels

Behind fishing vessels, either Herring Gulls, or Lesser Black-backed Gulls were the numeri-

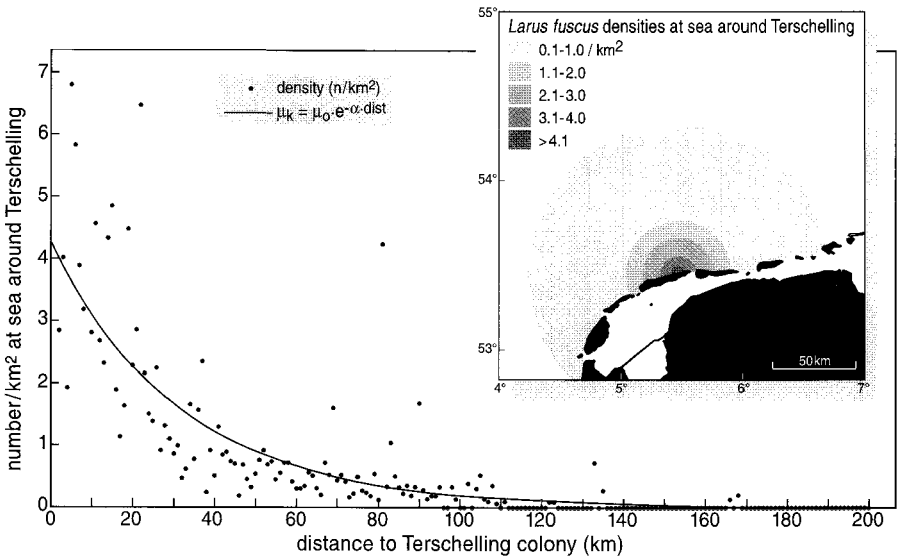

Fig.6. Abundance of adult Lesser Black-backed Gulls at sea (n/km^2) with increasing distance to the colony on Terschelling, as deduced from ship-based strip-transect counts, May-August 1987-1993 (from data published in Camphuysen & Leopold 1994). Shown are mean densities per stratum (+) and the expected mean density as a function $\mu = \mu_0.e^{-a.distance}$ of the distance, obtained by maximising the likelihood, assuming that counts were Poisson-like-distributed (solid line). Inset: impression of densities around Terschelling resulting from this analysis.

cally dominating species. The more powerful Great Black-backed Gulls formed a small minority and Kittiwakes occurred in numbers only near the colony at Helgoland. Fulmars were usually scarce and the individuals that turned up behind boats were usually moulting individuals (*i.e.* non-breeding birds or failed breeders; Cramp & Simmons 1977) in poor physical condition (fat reserves depleted). Skuas were absent or occurred in very small numbers. As a result, many fights for scraps were between Herring Gulls and Lesser Black-backed Gulls (31.4% of all recorded fights, n = 806). Scavenging commenced when the trawler resumed towing after having brought a catch on deck. Sorting and gutting marketable fish took place at a speed of approximately 5-7 knots. Herring Gulls and Lesser Black-backed Gulls took discards mainly close to the ship, constantly being on the wing and making shallow plunge-dives into the water. Attempts to pick up and swallow discards were successful in 82.7% of all cases in Lesser Black-backed Gulls (n = 1956) and in 82.4% of all cases in Herring Gulls (n = 848).

Prey selection and feeding success at the trawl

The discards fraction in beamtrawl fisheries, estimated at 5-10 kg of fish and benthic invertebrates on each kg of landed fish (Van Beek 1990, Camphuysen 1993b), is dominated by benthic invertebrates and flatfish. Benthic invertebrates were usually ignored by both Lesser Black-backed and Herring Gulls (0.3% consumed, both species combined; n = 2540; Table 7). Overall consumption rates of flatfish, roundfish and offal by these two gulls were respectively 30.5% (n = 1044), 70.7% (n = 1101) and 65.9% (n = 1217). Herring Gulls and Lesser Black-backed Gulls overlapped with respect to species and size selection of fish at the trawl (Camphuysen 1994). The number of flatfish taken by the two species was in accordance to expectation based on their relative abundance at the trawl (χ^2= 3.0, df= 1, n.s.). Herring Gulls, however, took significantly more offal particles than expected (= 18.03, df= 1, $p < 0.001$)

Table 5. Biometrics[1] and energy requirements[2] during the breeding season of adult Herring Gulls and Lesser Black-backed Gulls.

Species	Herring Gull			Lesser Black-backed Gull			
	Sex	Mean ± S.E.	n	Sex	Mean ± S.E.	n	Source
Mass (Wales)	♂	972 ± 13.1	47	♂	894 ± 11.3	38	Verbeek 1977
	♀	835 ± 11.7	35	♀	780 ± 11.9	41	
(Germany)	♂	1,051	80				Cramp 1983
	♀	864	80				
(Britain)	♂	977 ± 11.3	36	♂	880 ± 13.0	22	
	♀	813 ± 12.2	32	♀	755 ± 10.4	31	
Wing length	♂	423 ± 1.2	75	♂	425 ± 1.4	59	Verbeek 1977
	♀	400 ± 1.1	63	♀	407 ± 1.1	71	
Span	♂	1,409 ± 6.5	29	♂	1,408 ± 6.2	35	Verbeek 1977
	♀	1,325 ± 7.0	29	♀	1,332 ± 5.7	35	
Wing area	♂	2,106 ± 23.4	28	♂	2,053 ± 20.3	29	
	♀	1,838 ± 21.7	25	♀	1,848 ± 16.8	30	
Energetic requirements							
Mass	♂	1,000		♂	890		
(for calculation)	♀	850		♀	770		
BMR	♂	307.6 kJ		♂	282.4 kJ		*cf.* Aschoff & Pohl 1970
	♀	273.0 kJ		♀	253.9 kJ		
Daily requirements	♂	1538 kJ		♂	1412 kJ		*cf.* Drent & Daan 1980
	♀	1365 kJ		♀	1270 kJ		& Ellis 1984

[1] Measurements in mm; mass in grams; area in cm^2; wing load in grams/cm^2

[2] The relationship between *BMR* (kJ) and mass (W in kg) in non-passerines is: $BMR = 307.6 \cdot W^{0.734}$ (Aschoff & Pohl 1970). Seabirds from high latitudes have a greater BMR than tropical seabirds (Ellis 1984): assumed is 1.25 BMR for this latitude. The energy requirements of adults during the breeding season are estimated at 4 (1.25 BMR) (*cf.* Drent & Daan 1980).

and Lesser Black-backed Gulls took significantly more roundfish (χ^2= 10.93, df= 1, $p < 0.001$). Compared with other scavengers at the trawl, Herring Gulls could be classified as offal specialists, second only to the highly manoeuvrable Kittiwakes (Table 8). Herring Gulls obtained also more gadids than expected on the basis of numbers present at the trawl. Lesser Black-backed Gulls were particularly successful picking out gurnards, equalled only by Great Black-backed Gulls which tended to obtain the larger fish by robbing the smaller species.

Vulnerability to robbery

Of 342 fish handled by Herring Gulls and 959 fish handled by Lesser Black-backed Gulls, 50 and 104 fish respectively were stolen by other birds, 24 and 86 fish were dropped, and 268 and 769 fish were consumed (χ^2= 4.275, df= 2, n.s.). Up to seven scavengers handled individual discards. With regard to the first three birds handling a fish, numbers of Herring Gulls and Lesser Black-backed Gulls conformed expectation based on their relative abundance at the trawl (χ^2= 0.023, df= 1, n.s.). The number of Herring Gulls

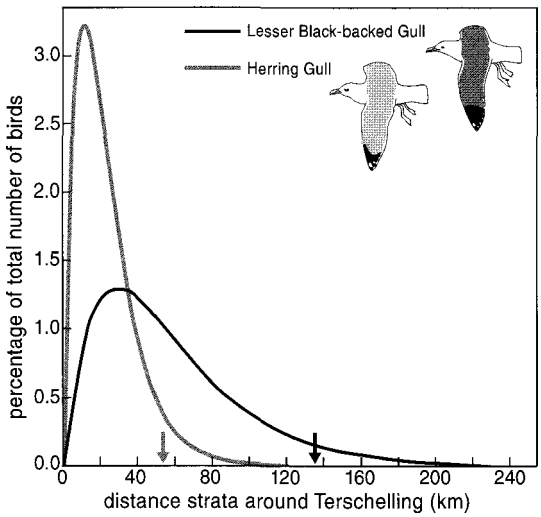

Fig.7. Percentage of total numbers of adult Lesser Black-backed and Herring Gulls at sea per radial stratum (km) with increasing distance to the colony on Terschelling. Total numbers were calculated from the expected mean density per stratum, obtained by maximising the likelihood, assuming that counts were Poisson-like distributed. Arrows indicate the range within which 95% of the calculated numbers at sea were found (grey arrow = Herring Gull, black arrow = Lesser Black-backed Gull).

handling fish for the 4th-7th time was significantly higher than expected on the basis of numbers present ($\chi^2 = 4.121$, df= 1, $p < 0.05$), suggesting that Lesser Black-backed Gulls gave up earlier. The vulnerability to robbery index of Herring and Lesser Black-backed Gulls, indicated that the latter lost 2.2x more fish through robbery than it obtained by robbing other species, whereas Herring Gulls obtained 1.4x more fish by kleptoparasitizing other species than they lost through robbery. Hence, Lesser Black-backed Gulls were clearly more vulnerable to robbery than Herring Gulls.

Table 6. Comparison of mean wing span, mass, minimum power speed (V_{mp} in m/s), maximum range speed (V_{mr} in m/s) and fuel consumption (kJ/km) in Herring Gulls and Lesser Black-backed Gulls (*cf.* Pennycuick 1989).

Species	Herring Gull		Lesser Black backed Gull	
	Sex	Mean	Sex	Mean
Span	♂	1,409	♂	1,408
	♀	1,325	♀	1,332
Mass	♂	1,000	♂	890
	♀	850	♀	770
V_{mp}	♂	9.1 m/s	♂	8.7 m/s
	♀	8.9 m/s	♀	8.5 m/s
V_{mr}	♂	15.1 m/s	♂	14.5 m/s
	♀	14.7 m/s	♀	14.1 m/s
kJ/km	♂	4.36	♂	3.80
	♀	3.80	♀	3.36

Table 7. Consumption of benthic invertebrates, flatfish, offal, and roundfish by Lesser Black-backed Gulls and Herring Gulls scavenging at a commercial beamtrawler, southeastern North Sea, June-August 1993. Expected numbers are based on relative abundance of these gulls at the trawl (mean Lesser Black-backed Gull 338, Herring Gull 54 individuals).

	offered (numbers)	LBBG (n)		HerrG (n)		consumption (%)
		obs	exp	obs	exp	
Benthic invertebrates	2540	7	6	0	1	0.3
Flatfish	1044	288	274	30	44	30.5
Offal	1217	627	692	175	110	65.9
Roundfish	1101	712	671	66	107	70.7

Table 8. Success indices of (common) scavenging seabirds at a commercial beamtrawler, June-July 1993. Success index calculated as number of items consumed divided by expected number of items based on numbers of birds at the trawl. The difference between the expected number of items consumed was compared with observed number, using a χ^2-test (with the null hypothesis of equal feeding success for all species).

Species	number of birds at the trawl (mean ± S.E.)	Success indices			
		offal $n = 595$	flatfish $n = 126$	gurnards $n = 275$	gadoids $n = 120$
Fulmar	5.7 ± 0.7	0.96	0.00	0.69	2.38 *
Herr. Gull	118.3 ± 19.2	1.33	1.09	0.35	1.34
Less. Bl.b Gull	369.8 ± 46.1	0.73	1.00	1.27	0.87
Gr. Bl.b Gull	23.5 ± 4.9	0.00	1.65	1.26	2.12
Kittiwake	26.4 ± 4.9	4.26	0.16	0.00	0.00
$\chi 2$		107.6	5.9	38.2	11.4
df		4	4	4	4
p		<0.001	n.s.	<0.001	<0.05

*High success index for Fulmar with respect to gadoids includes fish that were not instantly swallowed but pecked on and torn open to swallow intestines.

DISCUSSION

Breeding success, and also breeding numbers, are probably regulated through a density-dependent reduction in reproductive output resulting from reduced rates of food provisioning of chicks (*cf.* Furness & Birkhead 1984, Brandl & Gorke 1988). The provision of Herring Gull chicks at Schiermonnikoog with supplementary food in 1987 led to increases in reproductive output, resembling that of gulls breeding on Terschelling in the 1960s (Van Klinken 1992). The provision with supplementary food of Lesser Black-backed Gulls on Terschelling in 1992 increased the reproductive output in comparison with a control group of gulls (Spaans *et al.* 1994). However, this was not the case in 1993, when clupeids were more abundant off the coast than in 1992, indicating that the present low breeding success in most years is caused by a shortage of food. Reductions in the availability of marine fish may have been caused by changes in the shoaling behaviour of pelagic fish, fish stock collapses, declines in fishing effort and thus in the amount of discarded fish, or by increased intra- and interspecific competition of gulls at sea as a result of numerical increase of Herring and Lesser Black-backed Gull populations.

Scavenging behind fishing vessels is a common feature in both Herring and Lesser Black-backed Gulls. The sightings of Herring and Lesser Black-backed Gulls at fishing vessels during the breeding season indicate that the coastal zone is shared by these birds with respect to trawler visits, but with Herring Gulls numerically predominating within 5 km from the shore. The absence of Lesser Black-backed Gulls at many fishing vessels with Herring Gulls in the coastal zone, except near large colonies such as on Terschelling, indicates that this species generally avoids the nearshore area where Herring Gulls predominate. Further offshore, Lesser Black-backed Gulls are dominating and considering the numbers found at sea off the Frisian islands and numbers associated with offshore fishing vessels, this gull is primarily an offshore species. For scavenging gulls, the advantages of visiting fishing vessels near the coast are obvious. Short feeding trips

leave more time for adults to guard the chick, an important factor behind good breeding results (*cf.* Van Klinken 1992, Spaans *et al.* 1994). Birds that stay near land can soar along the dunes, waiting for fishing vessels within their field of vision, whereas the search for fishing vessels at sea requires prolonged periods of horizontal flapping flight. The energy requirements of horizontal flapping flight in large gulls may be as much as 7.5x the basal metabolic rate (BMR), whereas gliding flight costs only 3.1x BMR (Baudinette & Schmidt-Nielsen 1974, Ellis 1984). Finally, birds that stay near the coast have more possibilities to swap feeding areas (scavenging at fishing vessels, fishing at sea, feeding in the littoral zone, on land or in the Wadden Sea), whereas birds that fly out to sea can only choose between fishing and scavenging.

Data presented in this paper suggest that many Lesser Black-backed Gulls venture much further out to sea than expected from Herring Gull densities or anticipated numbers of fishing vessels. Densities of Lesser Black-backed Gulls at sea declined 3% per km away from the colony on Terschelling (Fig. 6), indicating a maximum feeding range of over 135 km (95% of all birds within 135 km of the colony). Such a feeding range is well above that found by Pearson (1968) and a single feeding trip would take nearly 7 hours of constant flight (at 40 km/h). The ability of Lesser Black-backed Gulls to fly greater distances than Herring Gulls has been acknowledged before (Verbeek 1977, Strann & Vader 1992) and the wing loading of Herring Gulls is such that they seem better off feeding closer to the colony (Verbeek 1977). However, the differences in fuel consumption per unit distance are rather small (Table 6) and the differences in flying distance are much larger than can be explained from inter-specific differences in the energetic cost of flight. In each species, differences in wing length are significant between sexes, from which it can be concluded that females are better adapted to fly longer distances than males. Indeed, in Lesser Black-backed Gulls on Terschelling, the mean duration of absence of breeding adults ranged from 85-90 minutes in males and 110-130 minutes in females (Spaans *et al.* 1994). It is important to emphasize that feeding trips of a duration of 7 hours have not been recorded in the Terschelling colony (A.L. Spaans pers. comm.). Although large groups of scavenging adult Lesser Black-backed Gulls were common at the far end of the maximum feeding range, the breeding status of these birds is thus uncertain. Considering the breeding population of the two species on the Wadden Sea islands (Table 1) and the total number of gulls at sea calculated from densities derived from strip-transect counts, it can be estimated that a minority of the nesting Herring Gulls (approximately 1:7) and virtually all Lesser Black-backed Gulls feed at sea. However, the assumption that all adults at sea off the Wadden Sea islands are associated with any of the breeding colonies may be wrong. In Herring Gulls it was found that part of the mature adults which show up in a colony early in the breeding season fail to start breeding or loose the eggs before hatching (Drost *et al.* 1961). The mere presence of adult birds at great distances of breeding colonies could thus be misleading when feeding ranges of breeding adults are estimated. The differences in length of the feeding range of Herring Gulls and Lesser Black-backed Gulls, however, is clearly reflected in the spatial aggregation of (large) colonies of both species (*cf.* Furness & Birkhead 1984): far apart in Lesser Black-backed Gulls, closeby in Herring Gulls (Table 1, Spaans 1987a, SOVON unpubl. data). Abundance estimates of Lesser Black-backed Gulls and fishing fishing vessels at sea showed that large numbers of gulls are found in areas which were not particularly rich in fishing vessels (Table 2-3), certainly not richer than the inner coastal strip. A long feeding range indicates that either interspecific competition is intense over a wide area along the coast (*cf.* Brandl & Gorke 1988), or that the trips are initiated by something else. The reason for moving that far out to sea, which cannot be fully explained by the relative abundance of fishing vessels, nor by avoidance of Herring Gulls, would than probably be another, offshore food resource. Recent studies in colonies have indicated that pe-

lagic shoaling fish such as small clupeids feature prominently in chick diets of Lesser Black-backed Gulls (Spaans *et al.* 1994) and such fish become only rarely available as discards in beamtrawl fisheries. Moreover, breeding success on Terschelling collapsed in the mid-1980s and remained low since that time, with the exception of 1986 and 1993, years in which small clupeids were rather abundant in food pellets of Lesser Black-backed Gulls (Noordhuis & Spaans 1992, Spaans *et al.* 1994). Future studies will have to show whether shoaling fish such as herring are in fact the main target of Lesser Black-backed Gulls moving away from the coast, with discards at fishing vessels as an additional source of food.

Fishing effort in the North Sea has increased enormously during this century particularly since the second World War (Daan *et al.* 1990). Despite an overall increase in fisheries, however, fishing effort in the southern North Sea has locally been reduced. The establishment of 'shipping lanes' in the late 1960s (changed in April 1987), may have removed quite substantial fisheries out of a ca. 15 km wide band off the Wadden Sea islands. Now that shipping intensities have increased during the last 25 years this effect may have gained importance. Secondly, in 1989, the regulation that large beamtrawlers were no longer allowed to fish within 12 miles (ca. 22 km) from land or within the plaice-box has removed substantial fisheries away from the coastal zone. These measures have probably reduced fishing effort and, hence, the availability of discards and offal for scavengers in the coastal zone. Breeding success of both Herring Gulls and Lesser Black-backed Gulls has declined in recent years and although food shortages were the key factor (Spaans *et al.* 1994), it is uncertain whether a possible reduction in fishing effort in the coastal zone has been responsible. Lesser Black-backed Gulls still feed mainly on marine fish, and may have expanded their feeding range, whereas Herring Gulls changed feeding habits and concentrated more on the littoral zone. Neither the vulnerability to robbery indices, nor the feeding success indices of both species did support the suggestion that Lesser Black-backed Gulls may have outcompeted Herring Gulls at (nearshore) fishing vessels. Future research will have to concentrate on natural feeding concentrations of these gulls off the Wadden Sea islands.

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SAMENVATTING

Men veronderstelt dat concurrentie met de Kleine Mantelmeeuw om visafval van vissersboten op zee zou samenhangen met teruglopende aantallen en verminderd broedsucces van de Zilvermeeuw op Terschelling. Om na te gaan of de Kleine Mantelmeeuw de Zilvermeeuw inderdaad heeft vedrongen achter vissersboten, werden zichtwaarnemingen van trawlers met zeevogelwolken verricht en geanalyseerd. Van de waarnemingen op zee kan worden afgeleid dat de Zilvermeeuw in de ondiepe Nederlandse kustwateren de meest talrijke en frequente zeevogelsoort is in het kielzog van trawlers. Kleine Mantelmeeuwen kwamen gemiddeld verder uit de kust voor. Hierdoor vermeden zij meestal de zone waar Zilvermeeuwen achter schepen domineerden. Achter trawlers bleken beide soorten een licht verschillende prooikeuze te hebben. Kleine Mantelmeeuwen hadden bij onderlinge gevechten meer te lijden van Zilvermeeuwen dan omgekeerd. Deze waarnemingen zijn in tegenspraak met de veronderstelling dat Zilvermeeuwen verdreven worden door inter-specifieke concurrentie om voedsel achter trawlers.

Het is niet waarschijnlijk dat de kleine verschillen in vliegcapaciteit tussen beide soorten wezenlijk hebben bijgedragen tot het enorme verschil in *feeding-range*. Het aanbod aan trawlers op grote afstand van de kust is niet bijzonder groot, zodat de motivatie voor Kleine Mantelmeeuwen om daar te foerageren, een andere moet zijn dan het aanbod aan bijvangsten.

Recente beperkende maatregelen voor de visserij hebben geleid tot afneming van de visserij-intensiteit voor de kust. Grote trawlers mogen niet meer binnen 12 mijl uit de kust vissen en 's zomers niet in de zogenaamde Schol-box. Bovendien is een verkeersscheidingsstelsel boven de Waddeneilanden ingesteld. Met name voor de Zilvermeeuwen van Terschelling is daarmee een belangrijk foerageergebied weggevallen, omdat daar de scheepvaartroute relatief dicht onder de kust ligt.