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Source: Ardea, 102(2) : 195-206

Published By: Netherlands Ornithologists' Union

URL: <https://doi.org/10.5253/arde.v102i2.a9>

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Consumption of discards by Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus* off the Belgian coast in the breeding season

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Sotillo A., Depestele J., Courtens W., Vincx M. & Stienen E.W.M. 2014. Consumption of discards by Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus* off the Belgian coast in the breeding season. *Ardea* 102: 195–205. doi:10.5253/arde.v102i2.a9

Fishery discards in the Belgian part of the North Sea are a source of food for Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus*. To understand the importance of discards for local *L. argentatus* and *L. fuscus* populations, single-item discard experiments were performed at four offshore distances from the gullery of the Port of Zeebrugge, at four different stages of the breeding season (May to August 2011). We compared flock composition during discarding with the distribution of Herring and Lesser Black-backed Gulls, with respect to offshore distance from the colony as reflected by an 11-year (2002–2013) dataset of standardised ship-based surveys. Consumption of discards depended on the type of fish that was discarded, but prey selectivity by adults was reduced during the chick rearing stage. A generalised linear mixed model identified the number of scavengers following the vessel, the proportion of adults and of Herring Gulls in the flock and the frequency of food robbery events interacting with the stage of the breeding season as affecting the variation in flat-fish consumption. Shifts in scavenger flock composition and discard consumption between stages of the breeding season are likely linked to variation in food requirements of the gull population along the season and to dispersal patterns towards the end of summer. Nutrient requirements of breeding adults peak during the chick rearing stage, making this a key period in terms of dependence of the breeding parents on discarded fish as food source.

Key words: fisheries, discards, scavenging gulls, North Sea, flock composition, *Larus argentatus*, *Larus fuscus*

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Breeding populations of *Larus* gulls have increased in the last decades along the Belgian coast (southern North Sea), from one pair in 1960 (Stienen *et al.* 2002) to a present population of more than 7000 pairs (INBO unpubl. data). These are mainly composed of Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus*. Local gull populations rely heavily on fishery discards: animal material caught by commercial fisheries that is subsequently returned to sea (as in Catchpole *et al.* 2005).

In the Belgian part of the North Sea, commercial fishing vessels mainly discard the products of bottom beam trawling: demersal flatfish (Sole *Solea solea*, Plaice *Pleuronectes platessa*, Dab *Limanda limanda*, etc.), roundfish (Whiting *Merlangius merlangus*, Bib *Trisopterus luscus*, etc.), and a range of benthic invertebrates (Garthe *et al.* 1996, Fonteyne & Polet 2002). Scavenging gulls prefer to consume gutted remnants and roundfish rather than flatfish or invertebrates (Garthe & Scherp 2003). Feeding conditions are highly

competitive at fishing vessels and scavenging birds often steal food from one another, in a behaviour referred to as kleptoparasitism or food robbery. The ability of an individual to capture – or steal – discarded material depends on its species and age, so that the age and species structure of a scavenging bird community determines its response to changes in the local availability of discards (Bertellotti & Yorio 2000).

A European ban on discarding of commercial fish species has been proposed within the reform of the Common Fisheries Policy (European Commission 2011, European Union 2013). This will reduce the current food subsidies of the Belgian gull population. Bicknell *et al.* (2013) highlight that current research should focus on understanding how seabird foraging could change as a consequence of this reform. Several studies have investigated the effects of ship-followers' flock size, the composition of the local aerial scavenger community and temporal and spatial variations on the consumption of discarded prey by seabirds (e.g. Berghahn & Rossner 1992, Camphuysen 1994, Oro & Ruiz 1997, Walter & Becker 1997, Garthe & Scherp 2003). In this paper, we explore the changes in number, composition and behaviour of the flock of birds follow-

ing a research vessel during experimental discarding of fish, throughout a breeding season (May to August 2011) along an offshore distance gradient from the major Belgian breeding large gull colony of the Outer Port of Zeebrugge.

We compared the flock composition recorded during experimental discarding to the foraging distribution of Herring and Lesser Black-backed Gulls as reflected by a 10 year (2002–2013) dataset of standardised ship-based surveys in the Belgian part of the North Sea. We then tested whether parameters such as flock size, scavenger age and species and stage of the breeding season influence the proportion of discarded flatfish that are consumed by scavenging gulls. Flock size, age- and species-structure were taken into consideration simultaneously to discriminate the effects of the abundance of scavengers from those of the flock composition. Flock age- and species-composition is hypothesised to have an effect through the different proficiency between age groups as well as between species in the handling of discarded material. The stage of the breeding season (hatching, chick-rearing, fledging and post-breeding) accounts for temporal variations in behaviour within the boreal summer period.

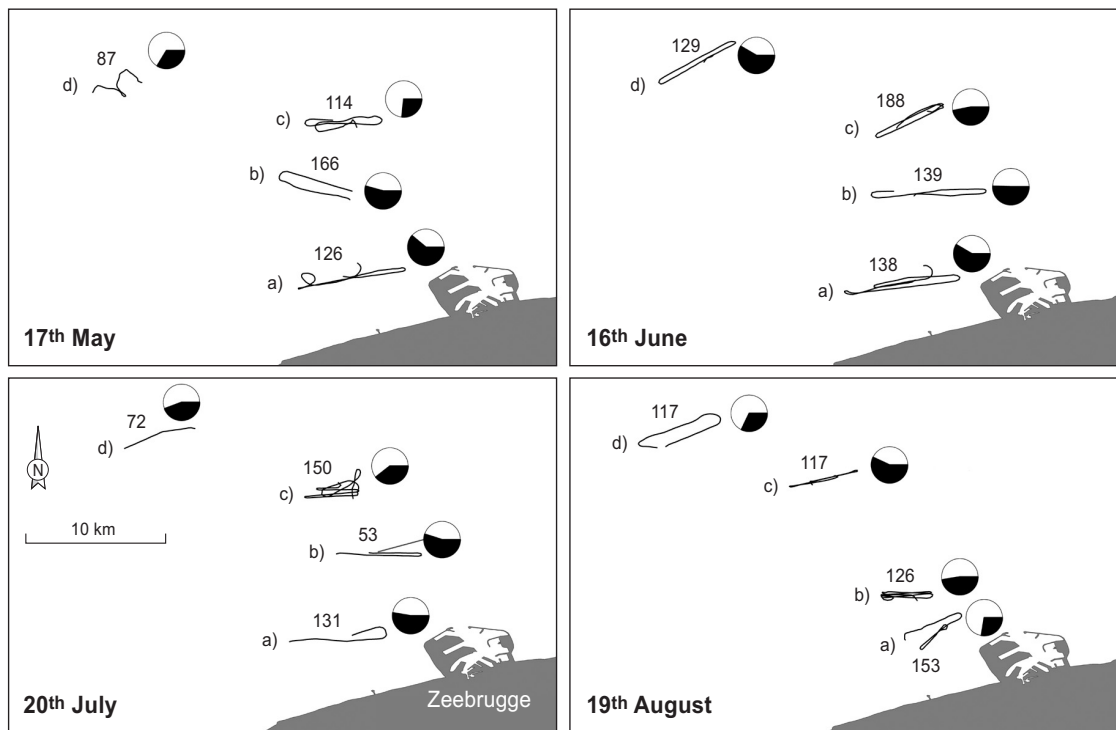


Figure 1. Trajectories of RV Zeeleeuw during the performance of discarding experiments, at: (a) 2.5 km, (b) 5 km, (c) 10 km and (d) 20 km off the Port of Zeebrugge on 4 days. Pie charts represent the fraction of flatfish (black) and roundfish (white) discarded. Numbers represent the total number of fish discarded.

We hypothesized that at different stages of the breeding season scavengers behave differently when exploiting discards, independent of their attendance in numbers to the vessel, due to changes in the need to forage for fish, which are in turn driven by reproductive nutritional demands. Interference competition is expected to reduce consumption rates at fishing vessels, with the scavengers fighting for, rather than actually consuming discarded biota.

METHODS

Study area

The Outer Port of Zeebrugge (51°20'N, 3°12'E), Belgium, hosts an internationally important colony of seabirds, mainly composed of gulls and terns (Stienen *et al.* 2002). The large gull breeding population is composed of Lesser Black-backed Gulls (c. 65%) and Herring Gulls (c. 35%; Stienen *et al.* 2002). Discard experiments were performed in the breeding season, on 17 May, 16 June, 20 July and 19 August 2011 (Figure 1), on board the research vessel 'Zeeleeuw', at locations situated 2.5, 5, 10 and 20 km off the Port of Zeebrugge. We repeated the experiments at different distances, moving away from the coast and colony, to account for the wider feeding range of Lesser Black-backed Gulls relative to that of Herring Gulls (Camphuysen 1995, Kubetzki & Garthe 2003). Experiments were held as close as possible to the Port of Zeebrugge to ensure that local birds (breeding adults) predominated within the feeding frenzies (Figure 2). All experiments took place under conditions of calm sea (wind force < 4 Bft, visibility 8–12 km) at daylight (between 10:00 and 17:00).

Experimental procedure

In single-item discard experiments, fish of different species and sizes were thrown from the aft of the research vessel. The fate of these 'experimental discards' were recorded as either sunken or consumed by a scavenging seabird. When an item was consumed, species and age class (calendar year) of the eating bird were determined by their plumage. Each detected robbery event was also recorded, as well as the species and age class of the kleptoparasite. Robbery events include both direct snatching from the beak and recapturing prey from the water surface after forcing its release. Before the start of an experiment, birds were attracted to the vessel by discarding offal. Experimental discarding started when more than 30 birds were flying close to the aft and had a total duration of 60 min, during which the research vessel steamed at a low pace

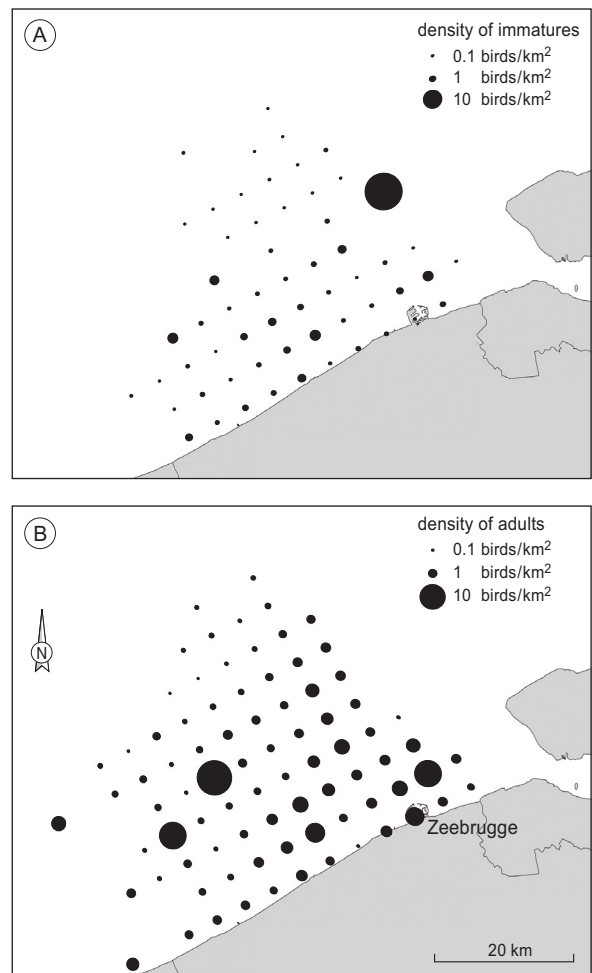


Figure 2. Densities of (A) immature (<5 calendar year) and (B) adult (>5 calendar year) Herring Gulls and Lesser Black-backed Gulls counted in the Belgian part of the North Sea, pooled over the period 2002–2013.

(0.8 ± 0.22 knots, i.e. 1.5 ± 0.41 km/h). Each experiment was carried out without interruptions, even if flock size decreased below 30 birds. Size and composition of the flock of birds following the vessel was estimated every five minutes, distinguishing between immature (juvenile to fourth calendar year) and adult birds of each species present. Most of the discarded fish (82%) were Whiting, Sole, Dab and Plaice, which have been reported as major discarded species in local beam trawl fisheries (Depestele *et al.* 2011). Other discarded species were gurnards (Triglidae), sandeels (Ammodytidae), Sprat *Sprattus sprattus*, gobies (Gobiidae) and Dragonet *Callionymus lyra*. Based on their similar dimensions, the latter group of species were considered as a single category, as were Dab and Plaice.

Comparison of at-sea census with counts of ship followers

The proportion of Herring Gulls against Lesser Black-backed Gulls was used as an approximation to scavenger flock species composition, given the dominance of these two species in the local aerial scavenger community. The sum of local densities obtained from standardized counts of seabirds at sea (as in Tasker *et al.* 1984, Method I) during the period 2002–2013 in the Belgian part of the North Sea, was converted to proportions of Herring Gulls against Lesser Black-backed Gulls in grids of 36 km². These proportions were calculated for both immature and adult birds pooled and for adults only. Each experiment was allocated the mean value of the Herring Gull to Lesser Black-backed Gull proportion from the cells at which it took place, and this census value was compared to the average flock composition recorded during experiments. Linear regression analyses were performed for (1) the local proportion of Herring Gulls according to census data against distance to the colony, (2) the proportion of Herring Gulls during experiments against distance to the colony, and (3) both data types for the proportion of Herring Gulls against each other. These regression analyses were performed on counts of adult and immature birds pooled, and for counts of adult individuals only.

Consumption of discards

To integrate all predictor variables into an analysis of variations in the proportion of flatfish consumed, a multiple Generalised Linear Mixed Model (GLMM) was used with a logit link function, using the R package MASS (Venables & Ripley 2002), based on the equation:

$$Y = b \times X + b' \times Z,$$

where the dependent variable *Y* is the proportion of flatfish consumed, *X* is the vector of explanatory variables considered (i.e. stage of the breeding season, flock size, proportion of adults in the flock, proportion of total captures that involved a food robbery event, proportion of flatfish discarded, proportion of Herring Gulls in the flock, and number of discarded fish), *b* is the vector of parameter estimates for the explanatory variables, *Z* is a random factor accounting for distance to the shore, and *b'* is the parameter estimate for the random effect factor. The model selection procedure was stepwise forward, based on deviances and on the *P*-values for differences between levels of included explanatory variables. All regression analyses were run in R v.2.14 (R Development Core Team 2011).

To further explore the effects of age class composition of the flock of scavengers, we assessed competition between immatures and adults by comparing their observed against expected captures. The number of items expected to be consumed by an age class within a stage of the breeding season was based on its relative abundance in the flock and the total amount of discarded items consumed by the flock. Expected captures were compared to those observed, under the null hypothesis that both age groups get a proportional share of the total captures. The expected number of items lost by an age group due to food robbery was as well compared to the observed number, under the null hypothesis that both age groups are victims of kleptoparasitic attacks proportionally to their abundance in the flock of scavengers. The significance of deviations from expected values was analysed with Chi-square tests for goodness of fit (Pearson 1900).

RESULTS

Comparison of at-sea census with counts of ship followers

Flocks of scavengers were dominated by Herring and Lesser Black-backed Gulls in all experiments (68 to 100% of birds) except on 20 July at 5 km distance (40% of birds). In the latter experiment, 59% of the flock was composed of Common Terns *Sterna hirundo*, but this species only accounted for 2% of the captures of discarded fish. The abundance of Herring Gulls relative to that of Lesser Black-backed Gulls decreases with increasing distance to the coast. This was observed for both the census data ($r^2 = 0.74$, $F_{1,13} = 37.2$, $P < 0.01$; Figure 3) and in the flocks during each experiment ($r^2 = 0.50$, $F_{1,14} = 13.9$, $P < 0.01$), and was maintained when considering only adult individuals, in census ($r^2 = 0.50$, $F_{1,14} = 14.0$, $P < 0.01$) and experimental data ($r^2 = 0.57$, $F_{1,14} = 18.5$, $P < 0.01$). Within adults, Herring Gulls were more dominant in the flocks of scavengers than predicted by the local census. This causes the relationship between relative abundances of both species for census data and counts of ship followers ($r^2 = 0.63$, $F_{1,13} = 21.9$, $P < 0.01$; Figure 4) to be absent when considering only adult individuals ($r^2 = 0.24$, $F_{1,14} = 4.46$, $P = 0.05$).

Consumption of discards

Roundfish was the preferred type of discard for aerial scavengers, followed by Sole, while Plaice and Dab were avoided (Table 1). Flatfish (mainly Sole, Plaice and Dab) showed the widest range of variation in the



Figure 3. Proportion of adult (A) Herring Gulls and (B) Lesser Black-backed Gulls in census data pooled over the period 2002–2013 for the Belgian part of the North Sea. Includes counts of both adult and immature birds.

proportions that were consumed, from 0% on 20 July at 20 km distance to 97% on 16 June at 2.5 km distance from the colony. A GLMM included (1) the flock size, (2) the proportion of Herring Gulls in the flock, (3) the proportion of adults in the flock, (4) the date at which the experiment took place (representa-

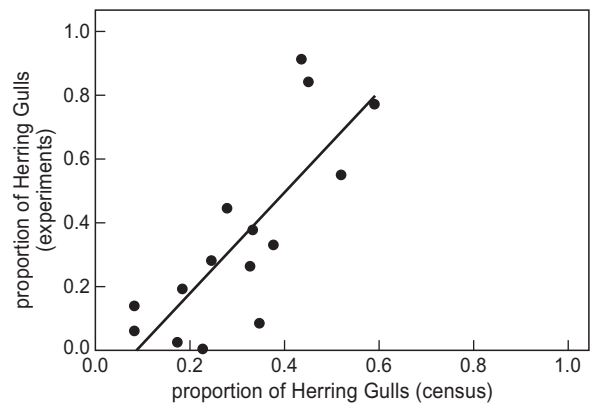


Figure 4. Relationship between the proportion of Herring Gulls in experimental and census data, age classes combined.

tive of the stage of the breeding season), (5) the proportion of total captures that were stolen and (6) the interaction between the intensity of food robbery and date of the experiment as significant parameters explaining the proportion of flatfish that was consumed (Table 2).

Flock size

Flock size was negatively related to the consumption of flatfish. Consumption was lower during experiments with high attendance (19 August) compared to those with less birds behind the vessel (experiments that took place on 16 June). Average flock size during experimental discarding ranged from 16 birds on 20 July at 5 km distance from the coastline, to 76 birds on 19 August at 20 km distance (Figure 5A). In census data for the Belgian part of the North Sea between the months of May and August (211 counts), numbers of ship followers range from 1 to 3016 birds, with an average of 385 birds per vessel, a median of 175 birds ($SD = 538$). The mean proportion of adults in the flock during experiments ranged from 6% on 19 August, at 5 km distance from the coast, to 98% on 20 July, also at 5 km distance. On average, largest flocks were observed on 19 August, coinciding with the smallest proportions of adults (Figure 5B).

Table 1. Average length and total number of discarded and consumed items of each defined type ($\pm SD$).

Fish category	Average length (mm)	Amount discarded	% Consumed	% Stolen
Whiting	200 \pm 46	829 \pm 22.99	88.75 \pm 5.73	7.72 \pm 4.95
Sole	191 \pm 37	354 \pm 15.49	69.60 \pm 11.24	6.04 \pm 5.19
Plaice and Dab	163 \pm 37	460 \pm 15.38	59.50 \pm 15.69	17.01 \pm 21.66
Other fish	124 \pm 49	408 \pm 20.04	75.01 \pm 9.86	1.25 \pm 1.72

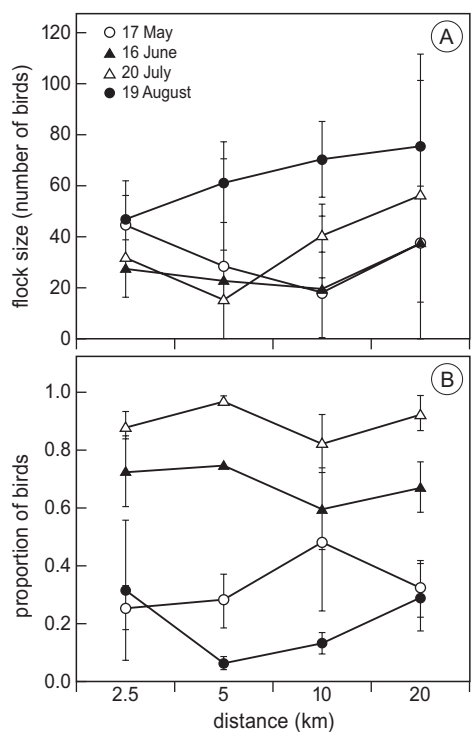


Figure 5. (A) Total number of Herring and Lesser Black-backed Gulls and (B) proportion of adults in the flock of scavengers during experiments plotted against distance from the coast. Error bars show SD.

Species structure

The proportion of Herring Gulls in the flock of scavengers ranged between 0 and 91% and showed a somewhat positive relationship with the overall consumption of flatfish. Larger proportions of consumed flatfish were therefore observed when flocks of ship followers were smaller and dominated by adult birds and/or Herring Gulls.

Age structure

An increase in the proportion of adults was related to increases in the consumption of flatfish. Adult scavenger gulls consumed consistently greater proportions of discarded roundfish compared to flatfish, except in experiments done on 16 June, when their prey selectivity appeared mitigated (Figure 6A). Among flatfish, adult scavengers consistently captured greater proportions of Sole than of Plaice and Dab. These trends were not seen in immature scavengers (Figure 6B). Adults were responsible for a greater proportion of the total captures than was expected from their respective density in the flock of ship followers in most of the experiments (Table 3). On 17 May and 16 June the difference between observed and expected captures of adults was between 1.4 and 4.5 times larger for round than for flatfish, when significant differences were found for both types of fish. Therefore, immature birds consumed discards at lower rates (Figure 6B), and this was especially true for roundfish.

Table 2. GLMM results for the effects on the proportion of total flatfish consumed of flock size, proportion of adults (>5 calendar year) in the flock, proportion of captures implying food robbery, proportion of Herring Gulls in the flock, stage of the breeding season, and the interaction between the breeding stage and proportion of captures that implied food robbery.

Factor	Estimate	SE	t-ratio	P
Intercept	6.49	2.19	2.96	0.060
Flock size	-0.10	0.01	-16.79	0.003
Proportion adults in the flock	19.96	0.92	21.63	0.002
Proportion stolen captures	-50.43	3.61	-13.96	0.005
Proportion Herring Gull in flock	10.91	0.43	25.15	0.002
Stage (hatching, 17 May)	-20.04	0.87	-23.14	0.002
Stage (chick-rearing, 16 June)	-21.24	1.03	-20.69	0.002
Stage (fledging, 20 July)	-28.19	1.17	-24.12	0.002
Stage (post-breeding, 19 August)	0.00	-	-	-
Stage × kleptoparasitism (hatching)	163.04	7.33	22.23	0.002
Stage × kleptoparasitism (chick-rearing)	74.55	4.60	16.22	0.004
Stage × kleptoparasitism (fledging)	106.93	4.75	22.52	0.002
Stage × kleptoparasitism (post-breeding)	0.00	-	-	-

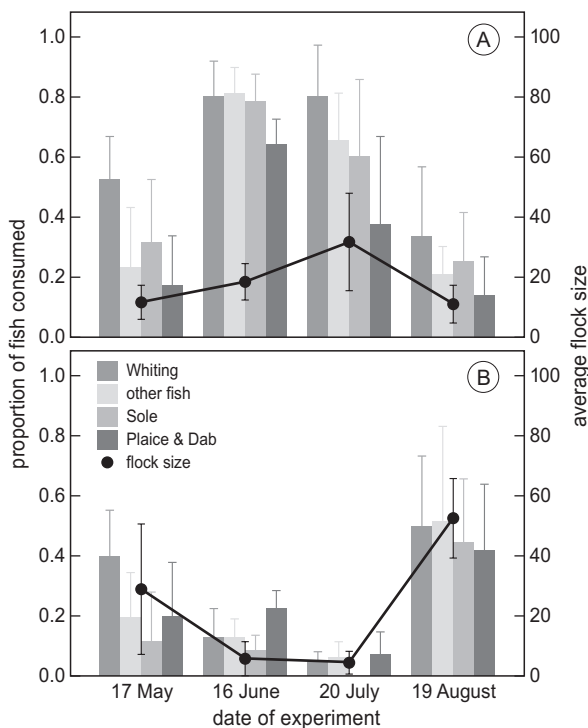


Figure 6. Average flock size (right axis) and proportion of each type of discarded fish consumed (left; \pm SD) by (A) adults and (B) immatures (<5th calendar year) per experiment day.

Food robbery

Regarding kleptoparasitism, Plaice and Dab were stolen more often than Whiting and Sole (Table 1). The category 'other fish', containing all the smallest species, was the least susceptible to be stolen. Food robbery was more intense when the overall consumption of flatfish was higher, except on 19 August, when the situation was inverted. Hence the significant interaction: On 19 August, 78% of the victims of food robbery were immatures, while this age group only accounted for 59% of captures, mostly performed by juveniles (Figure 7), that is, birds born in 2011. Immatures were therefore attacked more often than adults only at the post-breeding stage (Figure 8), when most of them were recently fledged juveniles.

DISCUSSION

We observed a substitution of Herring Gulls by Lesser Black-backed Gulls with increasing distance from the colony, both for our census data and for the scavenging community during experiments. This is in accordance with other studies done in the south-eastern North Sea during the breeding season. Camphuysen (1995) described this trend both in the flock of ship followers and in the densities at sea, and Kubetzki & Garthe (2003) related it to trophic niche segregation between the two species. The discarding vessel attracted birds

Table 3. Difference between the observed and expected number of captures ($n_{\text{obs}} - n_{\text{exp}}$) by adult (>5 calendar year) birds, and results of Chi-square tests for goodness of fit. Positive $n_{\text{obs}} - n_{\text{exp}}$ values imply a greater than expected number of captures. The experiment held on 20 July at 5 km distance from the coast was excluded because of small sample size.

Date	Distance (km)	Flatfish			Roundfish		
		$n_{\text{obs}} - n_{\text{exp}}$	χ^2_1	P	$n_{\text{obs}} - n_{\text{exp}}$	χ^2_1	P
17 May	2.5	9.27	10.69	< 0.01	18.79	29.02	< 0.01
	5	12.87	18.86	< 0.01	27.05	52.47	< 0.01
	10	0.12	0.63	0.43	20.92	23.96	< 0.01
	20	1.80	3.83	0.05	4.04	1.23	0.27
16 June	2.5	2.15	0.29	0.59	9.67	12.12	< 0.01
	5	8.80	5.81	0.02	14.68	14.32	< 0.01
	10	12.28	9.91	< 0.01	17.68	11.95	< 0.01
	20	7.51	4.37	0.04	14.88	16.95	< 0.01
20 July	2.5	-2.01	0.59	0.44	5.56	3.31	0.07
	10	-0.67	1.40	0.24	11.17	3.54	0.06
	20	0.11	0.11	0.73	-2.02	2.10	0.15
19 August	2.5	0.65	0.004	0.95	11.29	5.86	0.02
	5	3.73	4.53	0.03	3.23	1.65	0.20
	10	11.90	20.02	< 0.01	9.75	16.45	< 0.01
	20	10.92	23.71	< 0.01	47.71	124.24	< 0.01

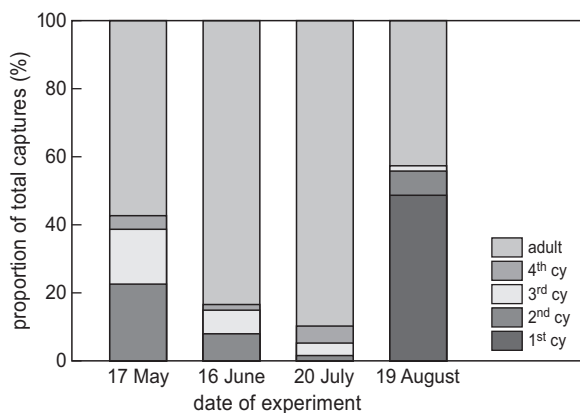


Figure 7. Proportion of the total captures per consumer age class, on the four days of the experiment. cy: calendar year.

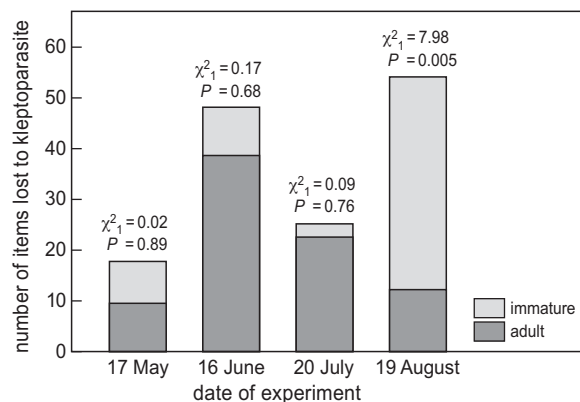


Figure 8. Number of items lost by each age class to other individuals, per experiment day, and results of Chi-square tests for goodness of fit between the observed number of items lost by immatures and the relative abundance of this age class in the flock.

from the immediate vicinity; if immatures are taken into account the flock composition at each experiment was dependent on the local community composition at a fine scale, as proposed by Skov & Durinck (2001). However, when considering only adult birds, Herring Gulls are more dominant within the actively scavenging birds at smaller distances from the colony, while Lesser Black-backed Gulls dominate the local adult community at all distances. This difference in species composition between the local at-sea census and the scavenger flocks may be due to the more coastal and generalist habitat use patterns of Herring Gulls, which roost and feed more often at land than at sea (Spaans 1971).

A GLMM analysis related the consumption of flatfish to (1) flock size, (2) species structure, (3) age structure, (4) stage of the breeding season and (5)

kleptoparasitism. Larger scavenger flocks, but an overall small consumption of discards, were observed at the end of the breeding season, after fledging, contrasting with the smaller but much more active flocks during chick-rearing. A greater vessel attendance by aerial scavengers did not foster the consumption of discards, but rather seemed to hinder it. Discard consumption was therefore more dependent on the frequency by which scavenging birds were capturing the discarded items rather than the amount of birds actively flying around the aft of the vessel. The number of active birds at the vessel during experiments remained within the range, and consistently below the average and median number of ship followers in the region as recorded by at-sea censuses. Considering the large variation in census data for scavenger attendance to vessels, the relatively small flock sizes recorded during our experiments could be related to spatial variability in vessel attendance within the Belgian part of the North Sea, which in turn could be due to the use of different fishing gears at a local scale, but evidence for this is lacking.

Excluding the effect of the distance from the coast at which discarding took place, a greater prevalence of Herring Gulls coincided with larger proportions of discarded flatfish being consumed. Although the Lesser Black-backed Gull is considered to be more manoeuvrable than the Herring Gull, and thus to compete better when feeding on discarded fish (Noordhuis & Spaans 1992, Furness *et al.* 1992), it is allegedly also more vulnerable to kleptoparasitism in mixed flocks (Furness *et al.* 1988, Garthe & Hüppop 1998). Because flatfish is more susceptible to food robbery, its exploitation would be more efficient in a flock dominated by Herring Gulls rather than by Lesser Black-backed Gulls.

The differences between observed and expected amounts of discards consumed by adults, reflect the consistently lower competitiveness of immatures (Verbeek 1977, Bertellotti & Yorio 2000), as well as the lower preference of adults for flatfish (Furness *et al.* 1988, Garthe & Hüppop 1994). Flatfish are a second choice prey because they have a longer handling time and are thus more susceptible to be stolen (Hudson 1989). The prevalence of adults, which are more proficient scavengers than immatures, therefore boosted the consumption of discarded flatfish. At the fledging stage, flocks were largely dominated by adults, while after the end of the breeding period, variation in the observed against expected number of captures was due to the abundance of recently fledged birds in the flock, which are less experienced in competing for prey than older birds (Spaans 1971, Verbeek 1977, Wunderle 1991). Differences in flock age composition between stages of

the breeding season might reflect the patterns of dispersion from the breeding grounds at Zeebrugge: second calendar year gulls abandon the colony earlier than third calendar year individuals, which in turn disperse earlier than adults and juveniles (see Van Waeyenberge *et al.* 2002).

Differences in food requirements of adults between stages of the breeding season are likely drivers of changes in vessel attendance by adult gulls and of their competitiveness when foraging. Therefore, temporal differences in the consumption of discards were found independent of the flock size or species composition. The chick rearing stage is a time of competition and consumption of discarded fish by adult Herring Gulls and Lesser Black-backed Gulls. Chicks from both gull species are fed extensively on fish (Spaans 1971, Furness *et al.* 1992, Garthe *et al.* 1999) and this energy-rich food source determines breeding success (Noordhuis & Spaans 1992). Consequently, vessel attendance and consumption of discarded fish by adults was most important during the period when they had to rear chicks until fledging. During this period, adults dominate the flock of scavengers, and are more competitive and less selective.

Food robbery had a negative effect on the overall consumption of discards at the post-breeding stage, when juvenile scavengers are abundant at discarding vessels. Kleptoparasitism might be a strategy used by younger birds to compensate for their competitive disadvantage towards older conspecifics (Verbeek 1977), although this behaviour does not always benefit immatures (Burger & Gochfeld 1981). In our results, adults obtain a net benefit by stealing food from juveniles, but not by stealing from other age groups.

Implications of a reduction in the availability of discards

A decrease in the availability of discards is expected to trigger demographic and behavioural changes in populations of aerial scavengers (Furness *et al.* 1992), whose effects might expand beyond this trophic guild (Votier *et al.* 2004, Wagner & Boersma 2011). The differential consumption of fish species means that a forthcoming discard ban may not only have an absolute effect on gull populations by decreasing the total amount of food available, but also an indirect effect as a change in discards composition will affect each species and age class differently, due to their different competitiveness (Bertellotti & Yorio 2000). The effect would be largest on the younger, less competitive, age classes. The demographic impact on the number of breeding pairs will be delayed, as adults are likely to

secure their survival due to their greater experience and adaptability. This effect was suggested by Pons & Migot (1995) for Herring Gulls exploiting human refuse. A buffered adult mortality will lead to a period when adults of an artificially enhanced population, deprived of one of their main food sources, might exploit other resources with a greater intensity, or look for alternative feeding grounds. Rock (2005) suggested that the rapid growth of urban Lesser Black-backed Gull colonies in the Severn Estuary was a consequence of changes in the local availability of fishery discards. However, it remains unknown as to what extent a reduction in fishery discards will have a significant effect on the local gull population breeding on the Belgian coast. Since the composition of discards varies spatially (Depestele *et al.* 2011), each type of discarded material has a specific nutritional value (Garthe *et al.* 1996), and scavenging seabird species are unevenly distributed at sea (Garthe & Hüppop 1994), the influence of fisheries on local populations of seabirds will vary spatially as well. Our results provide a snapshot on the composition and behaviour of flocks of scavenging gulls in the immediate vicinity of a breeding colony. Future research challenges include quantifying the importance of discards in sustaining current large gull populations at a local scale, and assessing the spatial variation in the use of this resource by aerial scavengers in the southern North Sea.

ACKNOWLEDGEMENTS

This research was a collaboration between the University of Gent, the Institute for Agricultural and Fisheries Research of Flanders (ILVO), and the Institute for Nature and Forestry Research of Flanders (INBO). The Flanders Marine Institute (VLIZ) provided logistical support for experiments on board RV Zeeleeuw. The authors would also like to thank Nicolas Vanermen and Hilbran Verstraete for their assistance during experiments. The experiments performed in this study comply with all applicable Belgian laws. The authors declare that they have no conflict of interest.

REFERENCES

- Berghahn R. & Rösner H. 1992. A method to quantify feeding of seabirds on discard from the shrimp fishery in the North Sea. *Neth. J. Sea. Res.* 28: 347–350.
- Bertellotti M. & Yorio P. 2000. Age-related feeding behaviour and foraging efficiency in Kelp Gulls *Larus dominicanus* attending coastal trawlers in Argentina. *Ardea* 88: 207–214.
- Bicknell A.W.J., Oro D., Camphuysen K.C.J. & Votier S.C. 2013. Potential consequences of discard reform for seabird communities. *J. Appl. Ecol.* 50: 649–658.

- Burger J. & Gochfeld M. 1981. Age-related differences in piracy behaviour of four species of gulls, *Larus*. Behaviour 77: 242–267.
- Camphuysen C.J. 1994. Flatfish selection by herring gulls *Larus argentatus* and lesser black-backed gulls *Larus fuscus* scavenging at commercial beamtrawlers in the Southern North Sea. Neth. J. Sea Res. 32: 91–98.
- Camphuysen C.J. 1995. Herring Gull *Larus argentatus* and Lesser Black-backed Gull *L. fuscus* feeding at fishing vessels in the breeding season: competitive scavenging versus efficient flying. Ardea 83: 365–380.
- Catchpole T., Frid C.L.J. & Gray T.S. 2005. Discards in North Sea fisheries: causes, consequences and solutions. Mar. Policy 29: 421–430.
- Depestele J., Vandemaele S., Vanhee W., Polet H., Torreele E., Leirs H. & Vincx M. 2011. Quantifying causes of discard variability: an indispensable assistance to discard estimation and a paramount need for policy measures. ICES J. Mar. Sci. 68: 1719–1725.
- European Commission 2011. Proposal for a regulation of the European Parliament and of the Council on the Common Fisheries Policy. European Commission, Brussels, <http://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX:52011PC0425>
- European Union 2013. Regulation (EU) No 1380/2013 of the European Parliament and of the Council of 11 December 2013 on the Common Fisheries Policy, amending Council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and repealing Council Regulations (EC) No 2371/2002 and (EC) No 639/2004 and Council Decision 2004/585/EC. European Union, Brussels, http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=uriserv:OJ.L_.2013.354.01.0022.01.ENG
- Fonteyne R. & Polet H. 2002. Reducing the benthos by-catch in flatfish beam trawling by means of technical modifications. Fish. Res. 55: 219–230.
- Furness R., Hudson A. & Ensor K. 1988. Interactions between scavenging seabirds and commercial fisheries around the British Isles. In: Burger J. (ed.) Seabirds & other marine vertebrates: competition, predation and other interactions. Columbia University Press, New York.
- Furness R.W., Ensor K. & Hudson A. 1992. The use of fishery waste by gull populations around the British Isles. Ardea 80: 105–113.
- Garthe S., Camphuysen C.J. & Furness R.W. 1996. Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. Mar. Ecol. Prog. Ser. 136: 1–11.
- Garthe S. & Hüppop O. 1994. Distribution of ship-following seabirds and their utilization of discards in the North Sea in summer. Mar. Ecol.-Prog. Ser. 106: 1–9.
- Garthe S. & Hüppop O. 1998. Foraging success, kleptoparasitism and feeding techniques in scavenging seabirds: does crime pay? Helgol. Meeresunters. 52: 187–196.
- Garthe S., Freyer T., Hüppop O. & Wolke D. 1999. Breeding Lesser Black-backed Gulls *Larus graellsii* and Herring Gulls *Larus argentatus*: coexistence or competition? Ardea 97: 227–236.
- Garthe S. & Scherp B. 2003. Utilization of discards and offal from commercial fisheries by seabirds in the Baltic Sea. ICES J. Mar. Sci. 60: 980.
- Hudson A. 1989. Interspecific and age-related differences in the handling time of discarded fish by scavenging seabirds. Seabird 12: 40–44.
- Kubetzki U. & Garthe S. 2003. Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. Mar. Biol. 143: 199–207.
- Noordhuis R. & Spaans A.L. 1992. Interspecific competition for food between Herring *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus* in the Dutch Wadden Sea area. Ardea 80: 115–132.
- Oro D. & Ruiz X. 1997. Exploitation of trawler discards by breeding seabirds in the north-western Mediterranean: differences between the Ebro Delta and the Balearic Islands areas. ICES J. Mar. Sci. 54: 695–707.
- Pearson K. 1900. On the criterion that a given system of deviations from the probable in the case of a correlated system of variables is such that it can be reasonably supposed to have arisen from random sampling. Philos. Mag. 50: 157–175.
- Pons J. & Migot P. 1995. Life-history strategy of the herring gull: changes in survival and fecundity in a population subjected to various feeding conditions. J. Anim. Ecol. 64: 592–599.
- R Development Core Team 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rock P. 2005. Urban gulls: problems and solutions. Br. Birds 98: 338–355.
- Skov H. & Durinck J. 2001. Seabird attraction to fishing vessels is a local process. Mar. Ecol. Prog. Ser. 214: 289–298.
- Spaans A.L. 1971. On the foraging ecology of Herring Gull *Larus argentatus* Pont. in the northern part of The Netherlands. Ardea 59: 73–187.
- Stienen E., Van Waeyenberge J. & Vercruyjsse J. 2002. Zilvermeeuw *Larus argentatus* en Kleine Mantelmeeuw *Larus fuscus* als broedvogels in Vlaanderen. Natuur.Oriolus. 68: 104–110.
- Tasker M., Jones P., Dixon T. & Blake B. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. Auk 101: 567–577.
- Van Waeyenberge J., Stienen E.W.M. & Vercruyjsse H.J.P. 2002. Kleur-ringproject van Zilvermeeuw *Larus argentatus* en Kleine Mantelmeeuw *Larus fuscus* aan de Belgische kust: overzicht van algemene resultaten. Natuur.Oriolus 68: 146–156.
- Venables W.N. & Ripley B.D. 2002. Modern applied statistics with S, 4th edn. Springer, New York.
- Verbeek N.A.M. 1977. Comparative feeding behavior of immature and adult herring gulls. Wilson Bull. 89: 415–421.
- Votier S., Furness R., Bearhop S. & Crane J. 2004. Changes in fisheries discard rates and seabird communities. Nature 427: 727–730.
- Wagner E.L. & Boersma P.D. 2011. Effects of fisheries on seabird community ecology. Rev. Fish. Sci. 19: 157–167.
- Walter U. & Becker P.H. 1997. Occurrence and consumption of seabirds scavenging on shrimp trawler discards in the Wadden Sea. ICES J. Mar. Sci. 54: 684–694.
- Wunderle J.M. 1991. Age-specific foraging proficiency in birds. In: Power D.M. (ed.) Current ornithology, 8th edn. Plenum Press, New York, pp. 273–324.

SAMENVATTING

Ongewenste vangsten in de visserij die in zee worden teruggegooid ('discards') vormen in het Belgische deel van de Noordzee een rijke voedselbron voor Zilvermeeuwen *Larus argentatus* en Kleine Mantelmeeuwen *L. fuscus*. Om het belang van de 'discards' voor de lokale broedpopulaties van beide meeuwensorten in te schatten, werd een aantal teruggooi-experimenten uitgevoerd. De experimenten vonden plaats op vier afstanden van de kust van Zeebrugge gedurende vier verschillende stadia van het broedseizoen (mei tot en met augustus 2011). We hebben de samenstelling van de scheepsvolgende 'discard'-consumenten tijdens de teruggooi-experimenten vergeleken met verspreidingskaarten van Zilver- en Kleine Mantelmeeuwen ten opzichte van de broedkolonie van Zeebrugge uit 2002–2013. Deze verspreidingsgegevens waren op een gestandaardiseerde wijze aan boord van een onderzoeksvaartuig verzameld. De consumptie van de door ons teruggegooiden 'discards' werd vooral bepaald door het type vis dat werd gebruikt. Dit selectieve foerageergedrag verminderde evenwel bij volwassen meeuwen in de periode dat hun jongen opgroei-

den. Een *Generalized Linear Mixed Model* werd gebruikt om de variatie in consumptie van teruggegooid platvis te verklaren. Het model wees de volgende verklarende factoren aan: (1) het aantal scheepsvolgers, (2) het percentage volwassen 'discard'-consumenten en Zilvermeeuwen in de zwerm, en (3) de frequentie waarmee de teruggegooiden 'discards' in de loop van het seizoen werd gestolen. De verschuivingen in de samenstelling van de scheepsvolgers en hun foerageergedrag op verschillende tijdstippen van het broedseizoen lijken erop te wijzen dat de voedselbehoefte van onze meeuwenpopulaties in de loop van het seizoen verandert of dat de verschuivingen verband houden met een ander verspreidingspatroon van de meeuwen naar het einde van de zomer toe. De voedselbehoefte van broedende volwassen meeuwen bereikt een hoogtepunt tijdens het opgroeien van hun kuikens. De beschikbaarheid van 'discards' als voedselbron lijkt in deze periode dan ook van essentieel belang voor de broedende meeuwen in Zeebrugge.

Corresponding editor: Kees Camphuysen

Received 11 June 2013; accepted 29 August 2014

