A COMPARATIVE STUDY OF THE DIET OF GUILLEMOTS *URIA AALGE* AND RAZORBILLS *ALCA TORDA* KILLED DURING THE *TRICOLOR* OIL INCIDENT IN THE SOUTH-EASTERN NORTH SEA IN JANUARY 2003

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Ouwehand J., M.F. Leopold & C.J. Camphuysen 2004. A comparative study of the diet of Guillemots *Uria aalge* and Razorbills *Alca torda* killed during the *Tricolor* oil incident in the south-eastern North Sea in January 2003. Atlantic Seabirds 6(3/S.I.): 147-164. In Jan-Feb 2003, some 4000 oiled seabirds washed ashore in The Netherlands following the *Tricolor* oil spill in the English Channel. Hundreds of corpses were collected and transported to laboratory facilities on Texel for autopsies. The opportunity was seized to conduct a diet study on two of the most numerous species among the oil victims, the Common Guillemot *Uria aalge* and the Razorbill *Alca torda*. Of 235 Common Guillemots stomachs that were examined, 59% contained prey remains that could be identified, while only 29% of 156 Razorbill stomachs contained such remains. The present study, the first that directly compares the winter diet of these two auks for the North Sea proper, reports a clear-cut difference in feeding ecology between the two species. Guillemots took a wider variety of prey fish (at least 24 different prey species, including both bottom-dwelling and mid-water species. Razorbills had a much narrower prey spectrum (>8 species). Razorbill diet was largely restricted to Sprats or small Herring. Prey diversity in Guillemots was as least twice as high as in Razorbills involved in the same oil spill. Clupeids (28% by number; 38% by mass), gadoids (20% by number; 47% by mass) and sandeels (31% by number; 10% by mass) were the most important prey in the Guillemots. For Razorbills, clupeids were of prime importance (72% of all prey identified; 88% of prey mass). Sandeels (24% by number; 11% by mass) were of secondary importance, while gadoids were absent in the Razorbill stomachs. Razorbills also had a much narrower prey size spectrum. Of the most commonly taken prey, Sprats and sandeels were on average larger in Guillemots than in Razorbills. The largest prey, Whiting and Herring of over 100 gram each, were predominantly found in adult male Guillemots. Stomachs with substantial prey remains ("full stomachs") were equally distributed over birds with different condition indices, as were completely empty stomachs. Large oiling accidents provide opportunities to conduct large-scale diet studies on several species of seabird simultaneously, but although major oiling incidents have happened time and again, relatively few have been seized to conduct such studies on any seabird. Our study shows also, that the large numbers of oil victims associated with major oil spills, should not be wasted, as they can provide very useful material for diet studies. Collecting sufficient numbers of oil victims should therefore be a priority in clean-up operations that usually follow the fouling of beaches and responsible authorities should be (made) aware of this.

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INTRODUCTION

Between 28 January 2003 and 9 February 2003, some 4000 oiled seabirds washed ashore in The Netherlands following the *Tricolor* oil spill in the English Channel. From the corpses counted during dedicated beached birds surveys that were carried out in response to the incident to assess the damage, a sample was collected and transported to laboratory facilities at the Royal Netherlands Institute for Sea Research on Texel for more detailed investigations including standard autopsies and stomach contents analyses (Camphuysen & Leopold 2004). The opportunity was seized to conduct a diet study on two of the most numerous species among the oil victims, the Common Guillemot *Uria aalge* and the Razorbill *Alca torda*, as little is known on the feeding ecology of these two auks in the southern North Sea. This paper reports on stomach contents of birds involved in this spill.

METHODS

A sub-sample of mainly heavily oiled, intact and rather fresh oil victims was dissected. Standard biometrical data were collected to assess sex, age, body condition at the time of death and possible origin of the casualties (see Camphuysen & Leopold 2004 for details). The amount of oil on the bird was noted for each individual. Un-oiled birds were excluded, as these were not part of this particular oil spill. Stomachs (gizzard and proventriculus) were taken out, bagged individually and kept frozen (-18°C) for later processing. Under the assumption that severely oiled individuals had died quickly and would probably be most useful to study the diet of wintering auks, such corpses were given priority during selection. Corpses from a rehabilitation centre were marked as such, because these birds may have been fed during treatment. However, when their stomachs were examined there were no indications of supplementary feeding and these birds were lumped with the others.

The stomachs were thawed and cut open for analysis. Stomach contents were rinsed with tap water into a glass jar. A controlled and gentle water overflow was used to wash off all organic soft material from the heavier hard parts that could be used for species identification (otoliths, fish bones, squid beaks etc.). All hard prey remains were sorted, dried, identified to the lowest possible taxon and measured if this could be used for prey size estimation. Fish were identified from their sagittal otoliths, pro-otic and pterotic bullae (herring family Clupeidae), atlas vertebrae (sandeels Ammodytidae), vertebrae and denticles (pipefishes Syngnathidae, Hooknose *Agonus cataphractus*, Lumpsucker *Cyclopterus lumpus*), spines (sticklebacks Gasterosteidae) and

Table 1. Correction factors used for worn otoliths (Leopold & Winter 1997, Leopold et al. *2001, Leopold & van Damme 2003).*

Tabel 1. Correctiefactoren om gesleten otolieten te kunnen herleiden tot de oorspronkelijke grootte (Leopold & Winter 1997; Leopold et al. *2001, Leopold & Damme 2003).*

Category of wear	Description	Correction factor
1	pristine (hardly any wear)	5%
2	sulcus and perimeter still intact (some wear)	10%
3	sulcus just visible (considerable wear)	15%
4	external features worn away (heavily worn)	mean size of conspecifics (see text)

preoperculae (dragonets Callionymiidae, Bull-rout *Myoxocephalus scorpius*). Other hard parts such as fish jaws were used when possible. Härkönen (1986), Watt *et al.* (1997), Leopold *et al.* (2001) and the Alterra/NIOZ reference collections of otoliths and fish bones were used for identification and for estimating original fish size and fish mass. *Ammodytes*-sandeels were not identified to species. All *Ammodytes* otoliths were treated as *Ammodytes tobianus* as this species is probably more common than *A. marinus* in nearshore waters of the SE North Sea. Invertebrates were identified from jaws (polychaetes) and horny beaks (cephalopods).

Otoliths were paired when possible and combined with other hard parts to identify individual prey. Fish size was estimated from each individual item (from the same presumed fish) separately, after correction for wear (Table 1) and the mean estimate for fish size was used subsequently. When the size of an identified fish could not be determined (incomplete or badly damaged hard remains), the mean size of that prey species was used instead, as derived from all stomach samples of either Guillemots or Razorbills.

Clupeoid bullae Two types of bullae of clupeids (Blaxter & Hunter 1982) were found: round, pro-otic bullae and potato-shaped pterotic bullae (Figure 1). Pro-otic bullae may come from either Herring *Clupea harengus* or Sprat *Sprattus sprattus*; pterotic bullae are lacking in Sprat. The bullae were sometimes found with clupeid otoliths, and were then matched with these to arrive at a minimum number of (specifically identified) fish for that stomach. However, in many cases bullae were found without clupeid otoliths present and then we followed a different approach. All bullae were classed as either large, medium or small. Large pro-otic bullae were *c.* 3-4 mm in diameter (casing exclusive) and in three cases, were found together with otoliths of large Herring (23.4, 24.9 and 27.6 cm total fish length). Small bullae were 1-2 mm in diameter and were found with both Herring and Sprat otoliths. Medium sized bullae of only three fish

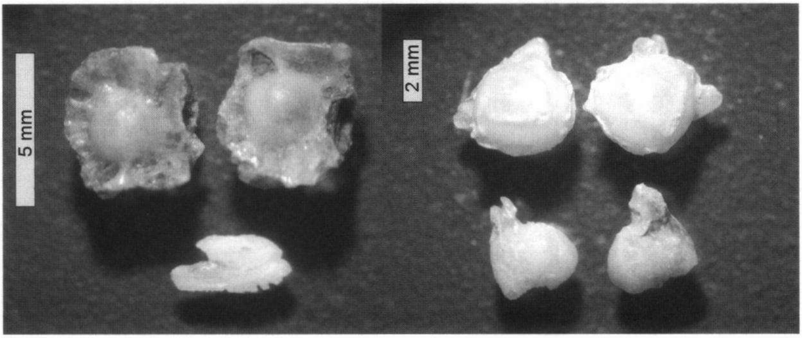

Figure 1. Large pro-otic bullae and Herring otolith (left panel) retrieved from a Guillemot stomach, representing a fish of 23.4 cm total fish length. Right panel: two large pro-otic bullae with two pterotic bullae from another Guillemot sample, representing a similarly sized Herring. Note that wear is more progressed in these bullae. Sprat only have pro-otic bullae but these are no larger than 2 mm in diameter (casing exclusive)

Figuur 1. Pro-otic bullae en otoliet van een grote Haring (23.4 cm lang) uit een maag van een Zeekoet (links). Rechts: een complete set van twee pro-otic en twee pterotic bullae van eveneens een grote haring, uit een andere Zeekoetmaag. Deze bullae zijn van Haring omdat de pro-otic bullae groter zijn dan 2 mm in diameter en omdat Sprot geen pterotic bullae heeft. NB: de bullae in het rechter plaatje zijn meer versleten en hebben daardoor meer van het omliggende bot verloren, maar de bullae zelf zijn nog grotendeels intact.

were found. In the first two cases, combinations of medium-sized pro-otic and pterotic bullae were found in a Razorbill and a Guillemot. In the third case, medium-sized bullae were found in a Guillemot stomach that further only contained the otoliths of an 18 cm long Herring. On this basis, we assigned large pro-otic bullae, all medium-sized bullae and all pterotic bullae to Herring (Table 2). We could now identify all large and medium Herring from either otoliths or bullae, but small clupeids that were only represented by pro-otic bullae could not be further identified. However, as only small pro-otic bullae were found, without any matching pterotic bullae, the vast majority of small clupeids that could only be recognised from the bullae in the stomachs, were probably Sprats.

Table 2. Types, sizes and numbers of clupeid bullae found in the stomachs of Guillemots and Razorbills. Small pro-otic bullae could have originated from either Sprat or small Herring, while all pterotic bullae and medium-sized and large pro-otic bullae originated from medium-sized (circa 18 cm total length) to rather large Herring (21-27 cm on the basis of otoliths found with these bullae).

Tabel 2. Types, grootte en aantallen bullae van haringachtigen zoals die werden aangetroffen in de magen van Zeekoeten en Alken. Kleine pro-otic bullae kunnen afkomstig zijn geweest van kleine Haring of Sprot, terwijl alle pterotic bullae en de grotere pro-otic bullae op basis van de bij deze bullae aangetroffen otolieten afkomstig moeten zijn geweest van Haring met een lengte van ongeveer 18 cm (medium bullae) tot zelfs 21-27 cm (large bullae).

Type	Shape	Size	**Guillemot** *n* fishes (*n* bullae)	**Razorbill** *n* fishes (*n* bullae)	Species
pterotic	potato	M	1 (1)	1 (2)	Herring
pterotic	potato	L	12 (20)		Herring
pro-otic	round	S	39 (70)	119 (231)	Sprat or Herring
pro-otic	round	M	2 (2)	1 (2)	Herring
pro-otic	round	L	23 (41)		Herring

Prey diversity For all prey species length and mass ranges are given in Table 3, with their relative abundance (RA) and frequency of occurrence (FO) in the diets of the Guillemots and Razorbills. In addition, relative mass (RM) was calculated, to weigh the contribution to the total ingested biomass. These indices were calculated according to:

$$RA = \frac{\sum_{k=1}^{s} n_{ik}}{\sum_{k=1}^{s} n_k} \qquad FO_i = \frac{\sum_{k=1}^{s} O_{ik}}{s} \qquad RM = \frac{\sum_{k=1}^{s} m_{ik}}{\sum_{k=11}^{s} m_k}$$

Where n_{ik} = (minimum) number of individuals of prey taxon *i* in stomach *k*

n_k = (minimum) number of individuals of all prey taxa in stomach *k*

O_{ik} = 0 if prey taxon *i* is absent in stomach *k*
1 if prey taxon *i* is present in stomach *k*

m_{ik} = (minimum) of total biomass of prey taxon *i* in stomach *k*

m_k = (minimum) of total biomass of all prey taxa in stomach *k*

s = total number of stomach samples that contained prey

***Table 3.** Reconstructed prey numbers (n), sizes (as range of total fish lengths, cm) and masses (range, g) in Guillemots. Fish masses of groups denoted with (*) were taken as averages of estimated masses of the relevant fish in the same sample. Fish that could not be identified to species (e.g. "Sprat or small Herring") were only included in the FO-index if no full species of this group (Herring or Sprat) were found in the same stomach.Two smal squid beaks were found, the masses lf these prey were guestimated (**).*

***Tabel 3.** Reconstructie van het aantal prooien (n), de prooigrootte (range, cm) en versgewicht (range, g) van de onderzochte Zeekoeten. De massa van met een asterisk (*) gemerkte prooisoorten werd geschat op basis van het gemiddelde gewicht van de relevante vissoorten binnen de zelfde vogelsoort in het monster. Vissen die niet op soort konden worden gedetermineerd (bijvoorbeeld "Sprot of kleine Haring") werden alleen in de FO-index opgenomen indien in een monster geen enkele prooirest op soort kon worden gebracht. . Er werden twee kleine inkvissnavels gevonden (**); de massa van deze twee prooien kon niet worden bepaald en werd geschat.*

Prey species	total *n*	fish length (cm)	fish mass (g)	RA	FO	RM
small Herring						
Clupea harengus	5	7.5 – 11.5	2.6 – 9.6	0.01	0.03	0
large+medium Herring	28	18.0 – 27.6	38.71 - 145.8	0.08	0.17	0.26
Sprat						
Sprattus sprattus	32	7.7 - 15.9	3.1 - 39.6	0.09	0.10	0.06
Sprat or small Herring (*)	39		14.68	0.11	0.10	0.06
Cod						
Gadus morhua	1	17.1	46.8	0	0.01	0
Bib						
Trisopterus luscus	7	11.4 - 19.1	16.9 – 89.5	0.02	0.05	0.04
Poorcod						
Trisopterus minutus	18	10.7 - 16.6	12.5 – 48.1	0.05	0.09	0.05
Bib or Poorcod (*)	2		33.37	0.01	0.01	0.01
Whiting						
Merlangius merlangus	47	12.0 - 27.1	12.9 – 158.8	0.13	0.28	0.37
Three-Spined Stickleback						
Gasterosteus aculeatus	1	7.8	4.1	0	0.01	0
Nilsson's pipefish						
Syngnathus rostellatus	4	< 15	0.5	0.01	0.03	0
Bull-rout						
Myoxocephalus scorpius	2	8.3 - 9.3	7.8 – 11.4	0.01	0.01	0
Hooknose						
Agonus cataphractus	2	14.9 - 14.9	23.9 – 23.9	0.01	0.01	0
Lumpsucker						
Cyclopterus lumpus	1	9	30	0	0.01	0

Prey species	total *n*	fish length (cm)	fish mass (g)	RA	FO	RM
Scad *Trachurus trachurus*	1	14.4	26.8	0	0.01	0
Greater sandeel *Hyperoplus immaculatus*	9	8.9 - 31.6	1.9 – 77.8	0.02	0.06	0.03
Sandeel *Ammodytes marinus* or Raitt's sandeel *A. tobianus*	104	5.0 – 24.0	0.2 – 46.0	0.28	0.36	0.07
Lesser weever *Echiichthys vipera*	1	14.5	37.3	0	0.01	0
Dragonet *Callionymus lyra*	17	5.3 - 12.8	1.0 - 14.0	0.05	0.08	0.01
Reticulated dragonet *C. maculatus*	19	6.6 - 9.8	2.0 – 6.4	0.05	0.03	0.01
Dragonet undet. (*)	3		4.47	0.01	0.02	0
Sand goby *Pomatoschistus minutus*	7	3.4 - 6.3	0.4 – 2.2	0.02	0.04	0
Common goby *P. microps*	7	3.9 - 5.4	0.6 – 1.8	0.02	0.03	0
Painted goby *P. pictus*	1	4.2	0.6	0	0.01	0
Goby undet. *Pomatoschistus sp.* (*)	2	3.7 - 5.7	0.5 - 1.7	0.01	0.01	0
Transparent goby *Aphia minuta*	6	3.9 - 5.1	0.3 - 0.9	0.02	0.01	0
Plaice *Pleuronectes platessa*	1	7.7	4.9	0	0.01	0
Squid undet. (*)	2		5	0.01	0.01	0
Total number of identified prey	369			369 prey	138 stomachs	9882 gram

RESULTS

Prey diversity in Guillemots and Razorbills Of 235 Common Guillemots stomachs that were examined, 59% contained remains that could be identified to specific fish or cephalopod prey (Table 3). A much smaller proportion of Razorbill stomachs (29% of 156 stomachs) contained such prey remains (Table 4). Remains of invertebrates other than squid (one small nereid worm, one small crab and several small bivalve and gastropod molluscs) were considered as secondary (fish) prey or gastrolites and were ignored. Guillemots took a wide variety of prey fish (24 or 25 different prey species in 138 non-empty stomachs), including both bottom-dwelling and mid-water species (Table 3). Razorbills had a much narrower prey spectrum (8 or 9 different species in 45 stomachs). Razorbill diet was largely restricted to Sprats or small Herring (Table 4). Most of these were probably Sprats, judging from the large number of small pro-otic bullae found in Razorbills (while small pterotic bullae were not found Table 2) and the fact that all clupeid otoliths in Razorbills were of Sprat.

Guillemot and Razorbill diets were also compared by calculating the average number of prey species per stomach for either species. For this comparison, we lumped all *Pomatoschistus* gobies, as we were not always certain of specific identification. Average (± SD) prey diversity was 1.53 ± 0.86 species per sample in Guillemots (n =138 non empty stomachs) and 1.24 ± 0.53 for Razorbill (n = 45), while maximum numbers of different prey species per stomach were 8 and 6, for Guillemot and Razorbill respectively. Although these statistics are rather similar for both species, many more prey species were found in the Guillemots (Tables 3 & 4). Note also, that in the Razorbills only one (species of) *Pomatoschistus* was found, compared to three species in the Guillemots. As the difference in total numbers of prey species found might be related to the much greater sample size in Guillemots we used a bootstrapping routine to examine the effect of sample size on total number of prey found. From the available stomachs with prey, we drew random samples and the procedure was repeated 100 times with replacement, after which average total numbers of prey species were calculated for different sample sizes. Because in both species, quite a few prey species were found in one or only a few more stomachs, the total number of species found increased with the number of stomachs examined and did not reach a plateau in either predator (Figure 2). 90% of the prey species involved would have been found in 35 Razorbill and 110 Guillemot stomachs, respectively. If only 45 stomachs with identifiable prey remains (the sample size for Razorbill) would have been available for Guillemot, 15 (±1.8) prey species would have been found, or 71% of those found in the 138 stomachs that were available for this species. This shows that prey diversity in Guillemots was as least twice as high as compared to the Razorbills involved in the same oil spill.

Clupeids (28% by number; 38% by mass), gadoids (20% by number; 47% by mass) and sandeels (31% by number; 10% by mass) were the most important prey in the Guillemots (Table 3). For Razorbills, clupeids were of prime importance (72% of all prey identified; 88% of prey mass). Sandeels (24% by number; 11% by mass) were of secondary importance, while gadoids were not found in the Razorbill stomachs (Table 4). The Frequency of Occurrence indices corroborate the finding, that clupeids and sandeels were

Table 4. Reconstructed prey numbers (n), sizes (as range of total fish lengths, cm) and masses (range, g) in Razorbills. See Table 3 for conventions.
Tabel 4. Reconstructie van het aantal prooien (n), de prooigrootte (range, cm) en versgewicht (range, g) van de onderzochte Alken. Zie verder de toelichting bij tabel 3.

Prey species	total *n*	fish length (cm)	fish mass (g)	RA	FO	RM
Large+Medium Herring *Clupeus harengus*	1	18.0	38.7	0.01	0.02	0.03
Sprat *Sprattus sprattus*	23	6.2 - 13.2	1.4 – 20.6	0.13	0.22	0.14
Sprat or small Herring (*)	107		8.48	0.59	0.29	0.71
Three-Spined Stickleback *Gasterosteus aculeatus*	2	5.0 - 6.1	1.0 – 1.9	0.01	0.04	0
Scad *Trachurus trachurus*	3	3.2 - 4.1	0.3 – 0.7	0.02	0.07	0
Greater sandeel *Hyperoplus immaculatus*	4	8.0 - 26.6	1.4 - 46.9	0.02	0.09	0.06
Sandeel *Ammodytes marinus* or Raitt's sandeel *A. tobianus*	40	3.4 - 13.3	0.1 – 6.8	0.22	0.18	0.05
Common goby *P. microps*	1	4.3	0.8	0.01	0.02	0
Squid undet. (*)	1			0.01	0.02	0
Total number of identified prey	182			182 prey	45 stomachs	1356 gram

important prey species for both the Guillemot and the Razorbill, while gadoids were also important, but for Guillemot only (Tables 3 & 4).

Prey sizes in Guillemots and Razorbills Razorbills also had a much narrower prey size spectrum. Most prey (166 of 182 fishes) were smaller than 10 cm total length, only one medium-sized Herring (18 cm) and two Greater Sandeels (of 22.2 and 26.6 cm) were larger than 15 cm. In contrast, less than one third of Guillemot prey were smaller than 10 cm (108 of 369), and 64 fishes were larger than 20 cm. Among these large prey were 23 large Herring and 9 Whiting with masses exceeding 100 gram. Of the most commonly taken prey by both Guillemots and Razorbills, both Sprats and *Ammodytes* sandeels were on average larger in Guillemots (Table 5). Again this shows that Guillemots took larger prey (t-tests: Sprat: $t=3.68$, $df=45$, $P<0.01$; sandeel: $t=9.79$, $df=115$ $P<0.01$).

Table 5. Average sizes (± 1 SD, cm; sample size in parentheses) of Sprat and sandeels (excluding Greater Sandeels Hyperoplus immaculatus*) taken by Guillemots and Razorbills. Fish sizes are reconstructed from otoliths found in the stomachs; fishes only represented by heavily worn otoliths were excluded.*
Tabel 5. Gemiddelde grootte (± 1 SD, cm, steekproefgrootte tussen haakjes) van Sprot en zandspiering (Smelt Hyperoplus immaculatus *uitgezonderd) in de magen van Zeekoeten en Alken. Visgroottes werden gereconstrueerd op basis van de in de maag aangetroffen otolieten, waarbij sterk gesleten exemplaren terzijde werden gelegd.*

Prey	Guillemot	Razorbill
Sprat	11.8 ± 2.00 (32)	9.7 ± 2.15 (23)
sandeels *Ammodytidae*	12.8 ± 3.72 (97)	7.8 ± 2.12 (38)

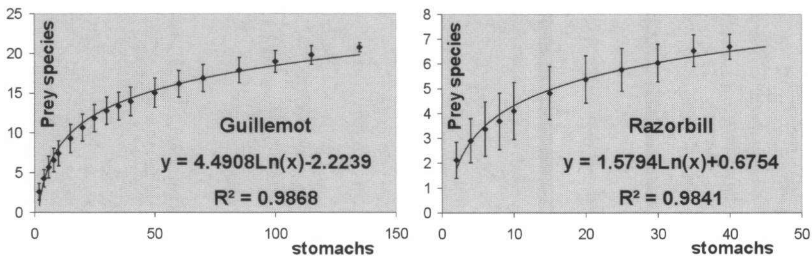

Figure 2. Average (± SD) numbers of prey types that would have been found in different sample sizes drawn from the total sample size of 138 stomachs with identifiable prey remains in the Guillemots (left) and likewise from 45 such stomachs from the Razorbills. A bootstrapping routine with 100 repetitions was used to estimate total numbers of different prey types likely to be found in different sub-sample sizes.
Figuur 2. Gemiddelde (± SD) aantallen prooisoorten dat gevonden zou worden bij een toenemend aantal steekproeven (magen) binnen het totale sample van 138 magen met identificeerbare prooiresten van de Zeekoet (links) of van 45 van dergelijke magen van de Alk. Een bootstrap-routine met 100 herhalingen werd gebruikt om het aantal prooisoorten te schatten bij verschillende monsternames.

Diet versus age and sex in Guillemots Numbers of non-empty stomachs across age classes were only sufficiently large in Guillemots to test the effect of the age or sex of the birds on diet. There was no clear trend in the average numbers of prey species per stomach with age (Table 6).

Adult Guillemots rarely had "full" stomachs (defined as containing fish flesh or >50 loose prey items), but full stomachs were found in a slightly higher proportion of non-adult birds. Of 95 adults with non-empty stomachs, 11 birds

Table 6. Average numbers (with standard deviation and sample size) of prey species identified per stomach in Guillemots of different ages.
Tabel 6. Gemiddeld (± SD) aantal prooisoorten per maag bij Zeekoeten van verschillende leeftijd.

	mean	SD	*n*
Adult	1.52	0.80	95
Immature	1.50	0.82	16
First winter	1.67	1.13	24

had full stomachs, while 7 out of 40 non-adults (immatures and juveniles combined, due to low sample sizes) had full stomachs (χ^2 = 14.93, P<0.005). This difference could be related to diet or to the average time between death and the moment the birds got contaminated with the oil. However, adult and non-adult diets were similar in that relative numbers of small or large Herring, small or large sandeels, dragonets, or gobies per stomach did not differ between age classes (χ^2 tests, P>0.1 in all cases). The only difference found between prey in adults and non-adults was that more adults had taken gadoids (45 gadoids found in 95 stomachs of adults, versus 8 gadoids in 40 non-adults; χ^2 = 5.37, P<0.05). This suggests that diet was not related to the probability of finding full stomachs, as gadoids were relatively large fish that would have taken relatively long to digest. Non-adults thus probably died quicker than adults, once they got contaminated because their prey would normally be digested more quickly, while their stomachs were more often still full.

Of the birds with non-empty stomachs that could be sexed during the autopsies (n=136), 93 (68%) were males. This percentage is close to that for all sexed birds (65% males, n=233) in which we examined the stomach contents. In the males, relatively many very large fishes (Herring or Whiting > 100 gram) were found, but the sample size was not large and this difference disappears if fishes > 50 grams or > 25 grams are included in the comparison (Table 7).

Diet versus condition index and amount of oil on the birds Stomachs with fish flesh or with large numbers (>50) of loose prey items were equally distributed over birds with different condition indices, as were completely empty stomachs, both in Guillemots and Razorbills (χ^2 tests, P>0.1 in all cases where sample size allowed for testing). We also tested whether the probability of finding a gadoid in a Guillemot stomach was related to the condition index of the bird, because gadoids are often considered as lean prey of low profitability. Birds in poor (CI from 0-3; n=38), moderate (4-6; n=71) and excellent condition (7-9; n=119) had similar probabilities of having remains of gadoids in the stomach (χ^2 = 3.07, P>0.1).

Table 7. Numbers of male and female Guillemots with remains of "large" fishes (masses over 100, 50 and 25 gram, respectively) in their stomachs. Given the sex-ratio of all birds with non-empty stomachs (68% males), the difference is only significant ($P<0.01$) if only fishes with masses exceeding 100 gram are considered.

Tabel 7. Aantallen mannelijke en vrouwelijke Zeekoeten met resten van grote vissen (van minimaal 100, 50 en 25 gram per stuk) in hun maag. Rekening houdend met het percentage mannetjes onder alle Zeekoeten met een niet-lege maag (68%) is het gevonden verschil alleen statistisch significant ($P<0.01$) als alleen de grootste vissen (van 100 gram of zwaarder) in de vergelijking worden betrokken.

Fish mass	*n*-males	*n*-females	expected numbers		% males	expected %	χ^2
>100	21	3	16	8	88	68	4.69
>50	36	12	33	15	75	68	0.87
>25	49	20	47	22	71	68	0.27

DISCUSSION

Guillemots and Razorbills both raise their chicks on rather small and fatty fish, such as clupeids and sandeels (Pearson 1968; Hedgren 1976; Bradstreet & Brown 1985; Harris & Wanless 1986; Leopold *et al.* 1992; Lyngs 2001). In winter, sandeels spend much time buried in sand and may thus be less available than in the breeding season, forcing the birds to turn to other prey. Winter diets of both species generally show a wider variety of prey species than in summer, including species of lower caloric density such as gadoids, gobies, sticklebacks, pipefishes and even nereid worms (Madsen 1957; Blake 1983, 1984; Blake *et al.* 1985; Durinck *et al.* 1991; Camphuysen & Keijl 1991, 1994; Leopold & Camphuysen 1992; Halley *et al.* 1995; Camphuysen 1998; Lyngs & Durinck 1998; Lorentsen & Anker-Nilssen 1999; Sonntag & Hüppop, manuscript AS). It should be noted, however, that studies in breeding colonies typically look at fish ferried into colonies and fed to chicks, and these might be different from fish eaten by the adults at sea (Camphuysen 2001). Adult Guillemots could take other prey, such as gadoids for self-feeding in the breeding season as well, but this would go largely unnoticed. Indeed, several studies in which adult Guillemots at sea were shot during the breeding and chick dispersal phase showed that gadoids were taken as food (Tasker *et al.* 1986; Anker-Nilssen & Nygård 1987; Leaper *et al.* 1987; Geertsma 1992).

It has been suggested that Sprat and Herring are key species for winter survival of auks (Blake 1984; Harris & Bailey 1992; Skov *et al.* 1992) and both the Guillemots and Razorbills examined here relied heavily on these clupeids.

However, a major and consistent difference between winter diets of Guillemots and Razorbills seems to be, that gadoids form a significant part of Guillemot diet, while Razorbills do not, or to a much lesser extent take these prey. Even if their caloric density is low, gadoids may in fact be profitable prey, as their large size more than makes up for this, as noted by Blake (1984). A large size may also be a constraint, however, both for small chicks in breeding colonies and for full-grown Razorbills. Experimental feeding trials have indicated that Razorbills are less well adapted than Guillemots to swallow large prey (Swennen & Duiven 1977). However, field studies on Razorbill winter diet and especially studies that cover both Razorbills and Guillemots in the same field situation, are rare (Blake 1983; 1984) or include only small numbers of Razorbills (Leopold & Camphuysen 1992) or are based on birds from different locations (Madsen 1957). Our study appears to be only the third that directly compares the winter diet of these two auks and the first that does so for the North Sea proper. We found a clear-cut difference between the two species, in that Guillemots took a much wider variety of prey species and prey sizes, including many relatively large fish (Herring and gadoids, particularly Whiting), while Razorbill diet was largely restricted to Sprat (possibly with an admixture of small Herring). The Razorbills were in excellent physical condition (Camphuysen & Leopold 2004) and this too clearly shows that Sprat was abundantly available in the general area struck by the *Tricolor* oil spill.

It must therefore be concluded that the Guillemots took gadoids because they "wanted" to. Alternative prey (Sprat) was available and it seems unlikely that Razorbills could have outcompeted the larger and more powerful Guillemots. In monospecific studies of Guillemot winter diets it has been suggested that finding large numbers of gadoid otoliths in the stomachs might be an artefact, due to the larger resistance of these thick otoliths to wear. This may be so, but it cannot explain the total absence of gadoid otoliths in the Razorbill stomachs. A physical limitation of Razorbills to catch and/or swallow large fish could explain this absence, but does not clarify why Guillemots take fish that they seemingly avoid in the breeding season. Blake (1984) suggested that the greater ability of Guillemots to include gadoids in their diet could be of great survival value, particularly during adverse winter conditions. In his study of wrecked birds, Razorbills also had taken mainly very small fish (sandeels and Sprat) and they probably had hunted for these in nearshore waters. There is some evidence that also in the Southern Bight of the North Sea Razorbills are comparatively common in nearshore waters (Camphuysen 1998) and this would, with their narrower diet, make the Razorbill a relatively vulnerable species.

Among the Guillemots, the largest fishes (>100 gram) were found predominantly in adult males, suggesting that not all Guillemots are equally equipped to catch and swallow large prey. Although our sample size of large fishes in sexed birds is small (Table 7), this result is largely in agreement with that of Lorentsen & Anker-Nilssen (1999) in their study on the diet of wintering Guillemots drowned in fishing nets in the Skagerrak.

Large oiling accidents provide opportunities to conduct large-scale diet studies on several species of seabird simultaneously, but although major oiling incidents have happened time and again, relatively few have been seized to conduct such studies on any seabird (Blake 1983; Furness 1994; Weir *et al.* 1995; Hughes *et al.* 1997). We had expected to find many birds with full stomachs, as most birds were very heavily oiled and must have died quickly with little time to digest their last meal. This was not found to be the case. Identifiable prey remains were found in less than half of the stomachs and this figure is no better than for wrecked birds as studied by Blake (1984). This suggests that auks do not feed around the clock and that many got hit by the oil some time after their last meal. Given the amount of oil on the birds, it seems unlikely that they suffered long, like many victims of chronic oil pollution that get fouled by smaller amounts of oil, clearly do. Still, a massive oil spill is no guarantee that all stomachs are full of recently ingested fish. Neither was the amount of oil on the bird within our sample related to the probability of finding a full stomach. Interestingly however, Razorbills had fewer full stomachs than Guillemots. This may have been partly related to a difference in diet, as the Razorbills had taken mainly small fish that would have had short retention times in the birds' stomachs. It may also be indicative of a different feeding strategy, with Razorbills only feeding at particular times (e.g. dawn and dusk when clupeids rise from the bottom to mid-water) as opposed to feeding around the clock (including at night, when birds might be more vulnerable to getting oiled).

Our study shows also that the large numbers of oil victims associated with major oil spills should not be wasted, as they can provide very useful material for diet studies. Large sample sizes are required to fully cover the range of prey species, particularly in species with a diverse diet. Such large sample sizes are usually available in full-blown oiling incidents. Our study gave no indication that heavily oiled birds provide better study material than birds that were not fully covered in oil and priority should thus probably be given to collecting adequate sample sizes across species, age classes and sex if possible (e.g. in seaduck). The probability of finding prey in an oil victim could be increased by also inspecting the gut rather than checking the stomach only. In an on-going study on the diet of Red-throated Divers *Gavia stellata* (Leopold *in prep.*), about equal numbers of prey remains are found in the stomach and gut and if the same holds for auks, we would have found about twice the number of prey items, had we inspected the whole digestive track of the birds in our sample. In our diet study, this was not possible as only the stomachs had been taken out of the birds during the general autopsies and when it was realised that many stomachs were empty, it was too late. In any case, oil victims should not be cleared off beaches without further ado, but kept for detailed studies, both to assess the damage on a population scale (see: Camphuysen & Leopold 2004) and to learn more about the diet of these elusive, offshore predators. Collecting sufficient numbers of oil victims should therefore be a priority in clean-up operations that usually follow the fouling of beaches and responsible authorities should be (made) aware of this.

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EEN VERGELIJKENDE STUDIE NAAR DE VOEDSELKEUZE VAN ZEEKOET *URIA AALGE* EN ALK *ALCA TORDA*, GESTORVEN ALS GEVOLG VAN HET TRICOLOR OLIE-INCIDENT IN DE ZUIDOOSTELIJKE NOORDZEE IN JANUARI 2003.

In januari/februari 2003 spoelden duizenden zeevogels aan op de kusten van Noord-Frankrijk, België en ZW Nederland, als gevolg van de olieramp van de *Tricolor* in Het Kanaal. Leden van de Nederlandse Zeevogelgroep konden enkele honderden lijken van veelal zwaar beoliede vogels bergen voordat de eveneens zeer actieve opruimploegen dit materiaal samen met de aangespoelde olie van het strand konden verwijderen. Hierdoor kon waardevol materiaal gered worden voor nader onderzoek. Dit materiaal werd door een grote snijploeg op het Koninklijk NIOZ op Texel verwerkt. De talrijkste slachtoffers bleken Zeekoet *Uria aalge* en Alk *Alca torda*, twee soorten die ook onder normale omstandigheden algemeen zijn bij tellingen van olieslachtoffers in het getroffen gebied. Beide soorten komen in de winter talrijk voor in de Zuidelijke Noordzee en lijken zo sterk op elkaar, dat ze tijdens bijvoorbeeld zeetrek- of vliegtuigtellingen vaak niet van elkaar onderscheiden kunnen worden. Een ecologische "wet" zegt echter dat twee soorten niet (lang) dezelfde niche kunnen bezetten. Als dit toch gebeurt zal uiteindelijk één van de twee de concurrentieslag van de ander winnen en deze verdrijven. Over het leven op volle zee van Zeekoet en Alk is echter nog maar weinig méér bekend, dan waar ze zoal voorkomen en in welke dichtheden. Studies aan hun voedselecologie zijn schaars en meestal beperkt tot slechts één van beide soorten. Een olieramp met veel slachtoffers die dik onder de olie zitten (en die dus vermoedelijk snel, soms nog met volle maag

zullen zijn omgekomen), in een streek met veel actieve zeevogelaars, vormt dus een buitenkans voor voedselecologisch onderzoek, hoe triest het sterven van grote aantallen olievogels ook moge zijn.

Honderden lijken werden in Zeeland verzameld en er konden magen worden onderzocht van 235 Zeekoeten en 156 Alken. Helaas waren de aantallen magen waar nog herkenbare voedselresten in zaten aanzienlijk lager: respectievelijk 138 (59%) en 45 (29%). Geconsumeerde prooien konden worden gedetermineerd en de prooigrootte kon worden gereconstrueerd aan de hand van allerlei specifieke harde voedselresten. Vaak gaat het daarbij om otolieten (gehoorsteentjes, gemaakt van zeer hard kalk-achtig materiaal en met een soort-specifieke vorm aanwezig in alle soorten beenvissen) en bolvormige gasblaasjes van botachtig materiaal (*bullae*) die zich in de schedel van Haring *Clupea harengys* en Sprot *Sprattus sprattus* bevinden.

Zeekoeten en Alken bleken opmerkelijke verschillen in hun menukeuze te vertonen. Zeekoeten hadden een veel breder dieet, zowel in aantallen soorten vissen (zeker twee maal zo veel prooisoorten, gecorrigeerd voor het verschil in aantallen onderzochte magen) als een grotere variatie in de grootte van de gegeten prooidieren. Alken richtten zich zeer sterk op Sprot en wellicht kleine Haring (samen goed voor 72% van alle gevonden vissen; 88% van alle prooimassa). Zandspieringen *Ammodytes* spp. (24% van de aantallen prooien; 11% van hun gezamenlijke massa) vormden de voornaamste aanvulling. In Zeekoeten werden zeker 24 verschillende prooisoorten teruggevonden, waaronder zowel vissoorten die bij de bodem leven als soorten die hoger in de waterkolom voorkomen. Ook voor Zeekoeten waren Haring en Sprot (28% van de totale prooiaantallen; 38% van de totale massa) en zandspieringen (31% van de aantallen; 10% van de totale massa) belangrijk, maar er werden ook veel kabeljauwachtigen (20% van de aantallen en omdat dit vaak relatief grote vissen waren 47% van de totale prooimassa) gevonden. In de Alken werd geen enkele kabeljauwachtige gevonden en ook waren de gevonden haringachtigen en zandspieringen gemiddeld kleiner dan die in de Zeekoeten. Zeekoeten kunnen verrassend grote vissen aan: er werden resten gevonden van 23 haringen en 9 wijtingen van meer dan 100 gram zwaar. De grootste gevonden vissen waren ruim 27 cm lang (Tabel 3). De meeste grote vissen (>100 gram) werden gevonden in volwassen mannetjes Zeekoeten, maar overigens waren er onder de verschillende categorieën Zeekoeten (ingedeeld naar leeftijd, geslacht, hoeveelheid olie op de veren en lichaamsconditie) nauwelijks meetbare verschillen in de voedselkeuze. De aantallen Alken met voedselresten in de maag waren te klein voor dit soort onderlinge vergelijkingen.

Grote olierampen kunnen dus benut worden voor onder meer voedselonderzoek aan zeevogels, onderzoek dat buiten het broedseizoen op andere manieren niet of nauwelijks te doen is. Het interessante van grote olierampen is, dat tegelijkertijd, in hetzelfde gebied, meerdere soorten zeevogels samen kunnen worden onderzocht, waardoor we ook meer te weten komen over hun onderlinge verschillen en overeenkomsten. Overheden geven bij olierampen prioriteit aan het opruimen van de rommel, waarbij dan meestal wel het kind (de vogels) met het badwater wordt weggegooid. Deze studie toont aan dat het de moeite loont om alert te zijn bij olierampen en vogels voor nader onderzoek te verzamelen. Het is zeker, dat we in de toekomst opnieuw te maken zullen krijgen met olierampen, de vraag is alleen: waar en wanneer? Van olievogels valt veel te leren; het is dus zaak om steeds weer alert te zijn bij dergelijke gebeurtenissen. Door onderzoek te doen aan de getroffen vogels kunnen we inzicht krijgen in hun leven op zee, waardoor de dieren dan tenminste niet helemaal voor niets zijn omgekomen.

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