SNACKS FROM THE DEPTH: SUMMER AND WINTER DIET OF COMMON GUILLEMOTS *URIA AALGE* AROUND THE ISLAND OF HELGOLAND

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Sonntag, N. & O. Hüppop Snacks from the depth: summer and winter diet of Common Guillemots *Uria aalge* around the Island of Helgoland. Atlantic Seabirds 7(1): 1-14. *Stomach contents from 53 Common Guillemots* Uria aalge *beached at the Island of Helgoland in the southeastern North Sea were examined for prey remains. In winter 2000/2001, the prey spectrum was quite diverse. Remains of species belonging to ten different families of teleost fishes were found, with pipefishes, gobies, sandeels and clupeids being the most abundant prey. Invertebrates contributed only 1 % of all prey items. The diversity was considerably smaller in winter 2001/2002, when clupeids and sandeels had the highest numerical abundance and only three other families were found. The number of sandeels and clupeids in the stomachs might be connected with water temperature. When these fish families were present in the stomachs, the water temperature on the day before collecting the dead Guillemots was significantly higher than when these fish were absent in both winter periods. The few samples collected in summer contained mainly sandeels and clupeids, fish species which are also brought to the colony for display and to feed the chicks. However, the fishes found in the stomachs of the adult birds were smaller than fishes carried to the breeding ledges. Additionally, a dragonet and a cephalopod were found in the stomachs, prey that have never been observed in the colony. This confirms our assumption that observations of the fishes brought to the colony are not representative for the diet of adults. Adult Guillemots deliver relatively large fishes of high caloric density to the chicks. During self-feeding, they are much more opportunistic and also consume smaller and leaner prey. This is in accordance with Central Place Foraging Theory. Difficulties in the methods employed and the effect of oiling on diet composition are also discussed in this study. While oiling seemed to have no influence on the total number of prey items found in the stomachs of the dead Guillemots, we found sandeels and gobies more frequently in oiled and pipefishes more often in unoiled birds.*

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INTRODUCTION

Common Guillemots *Uria aalge* have been breeding at Helgoland in the southeastern North Sea (54°11′ N, 7°53′ E) since at least the beginning of the 19th century (Gätke 1900). After a 20-year-increase (Hüppop 1997), the colony

is today more or less stable with some 2000 to 2500 breeding pairs (Dierschke et al. 2003). The colony is situated at a considerable distance from other North Sea Guillemot colonies and the prey base may thus be different. There is limited information on prey delivered to chicks or used for display in the breeding season. Leopold *et al.* (1992) and Grunsky-Schöneberg (1998) observed that only sandeels and clupeids, fishes of high energetic value, were brought to the breeding ledges at Helgoland. Similar to the situation around most Guillemot colonies, there is no published account on Guillemot diet around Helgoland in winter. Guillemots are present around the island throughout the year, apart from August (Stone et al. 1995, own observations, German Seabirds at Sea Database, Vers. 3.0), but there is no *a priory* reason to believe that the prey delivered to the chicks represents the diet of the birds during self-feeding, either in the breeding season or at other times of year. According to Central Place Foraging Theory, we assume that a forager increases its fitness by maximizing the rate of delivery of energy e.g. to the breeding place (Orians & Pearson 1979). In a single-prey loader such as the Guillemot, this can be achieved by maximizing the size of the prey brought by the parent to the colony. But why should adult Guillemots not use other, less valuable prey for themselves, especially if it is abundantly available? If fishes need not to be carried off to the breeding ledge, the birds can profitably ingest fish of smaller size or lower caloric density.

Guillemots catch and swallow their prey under water, making direct observations impossible. Examination of stomach contents is an alternative method to study the diet of seabirds (Duffy & Jackson 1986). But, due to ethical reasons, birds should not be killed, which makes obtaining sufficiently large sample sizes difficult. There are various methods to take samples from living birds (for reviews see Duffy & Jackson 1986 and Camphuysen 1990a). However, on Helgoland Guillemots breed on brittle sandstone cliffs where it is neither possible to catch living birds nor to collect faeces. Furthermore, this species does not produce pellets. Therefore, we used beached birds for this study, and dissected their stomachs. This paper presents data on the winter and summer diet of adult Guillemots and discusses the limitations of diet studies using beached birds and the effect of oiling on diet composition.

METHODS

From November 2000 to June 2002 53 carcasses of beached Guillemots were collected at Helgoland. In the 'winter' months (October to March) 49 birds were found, 40 in winter 2000/2001, nine in winter 2001/2002. Four Guillemots were collected in the 'summer' months (April to September), one in summer 2001 and three in summer 2002. 25 of the collected Guillemots were oiled, one bird was caught in fishing gear, one was killed when found with a broken wing, 26

birds died from unknown reasons. The winter sample contained immature and adult birds, the summer sample only adult Guillemots. Birds were aged by feather characteristics (moult of the greater upperwing coverts, white tips on the greater underwing coverts) and the *bursa Fabricii* (presence/absence, size) according to Camphuysen (1995a).

The birds were opened, and their proventriculus and gizzard removed and kept frozen until examination. Fishes were identified from their sagittal otoliths and vertebrae. In addition, the pro-otic bullae of clupeids, the atlas vertebrae of sandeels and the bony plates of pipefishes helped to identify the family. For the identification of otoliths, Härkönen (1986) and Leopold et al. (2001) were used. Vertebrae were identified according to Watt *et al.* (1997). The station's reference collection was additionally used for identification. Invertebrates were identified by jaws (polychaetes), claws (crustaceans), horny bills (cephalopods) and shells (molluscs) but not determined to species. Remains of plants were only counted.

For a quantitative interpretation, otoliths and clupeid bullae were counted. Two items of the same size and feature were assumed to represent one fish. The characteristic atlas vertebrae of the family Ammodytidae additionally gave information about the number of sandeels represented in the sample. If only vertebrae of a given fish species were found, it was assumed that the bird had eaten one fish of that species or family. For invertebrates the number of jaws, claws and bills gave reference to the ingested individuals.

From the summer sample, lengths of apparently intact otoliths of sandeels and widths of apparently intact otoliths of clupeids were measured with a digital calliper and corrected for a 5 % wear of the otoliths (see Camphuysen 2001). These measures were used to calculate the fish length according to Härkönen (1986).

Possible effects of oiling on the number and species of food items were investigated in winter 2000/2001, when the beaches were controlled daily and the dead birds did not lie there for more than a day.

RESULTS

Diet composition in the winter 2000/2001 In 40 stomachs, fishes of ten different families comprised 99 % of all food items (Table 1). Pipefishes, gobies, clupeids and sandeels were the most common prey. Remains of four hooknoses and three three-spined sticklebacks *Gasterosteus aculectus* occurred in the stomachs. Other species (of the families Carangidae, Gadidae, Pholidae, Pleuronectidae) were found only once. The samples contained five invertebrates (two polychaete worms, a very small gastropod and a very small crab) and ten pieces of plants.

		Winter 2000/2001		Winter 2001/2002	
Number of stomachs (with food remains)		40 (37)		9 (8)	
Number of prey items (identified)		374 (355)		47 (44)	
		Frequency of occurrence (%)	Numerical abundance (%)	Frequency of occurrence (%)	Numerical abundance (%)
Fishes					
Agonidae	*Agonus cataphractus* (Hooknose)	4 (10)	4 (1.1)		
Ammodytidae	*Ammodytes* spec. a/o *Hyperoplus spec.* (Sandeel)	14 (35)	44 (11.8)	4 (44.4)	10 (21.3)
Callionymidae	*Callionymus* spec. (Dragonet)			1 (11.1)	1 (2.1)
Carangidae	*Trachurus trachurus* (Horse mackerel)	1(2.5)	1 (0.3)		
Clupeidae	*Clupea harengus* (Herring) / *Sprattus sprattus* (Sprat)	19 (47.5)	27 (7.2)	5 (55.6)	30 (63.8)
Gadidae	*Merlangius merlangus* (Whiting)	1 (2.5)	1 (0.3)		
Gasterosteidae	*Gasterosteus aculeatus* (Three-spined stickleback)	2 (5)	3 (0.8)	1 (11.1)	1 (2.1)
Gobiidae	*Pomatoschistus* spec. (Goby)	12 (30)	124 (33.2)	1 (11.1)	1 (2.1)
Pholidae	*Pholis gunellus* (Gunnel)	1 (2.5)	1 (0.3)		
Pleuronectidae	*Hippoglossoides platessoides* (Long rough dab)	1 (2.5)	1 (0.3)		
Syngnathidae	Pipefishes	19 (47.5)	145 (38.8)		
Unidentified			19 (5.1)		3 (6.4)
Invertebrates					
Polychaeta	Polychaete worms	2 (5)	2 (0.5)		
Crustacea	Crabs	1 (2.5)	1 (0.3)		
Gastropoda	Molluscs	1 (2.5)	1 (0.3)	1 (11.1)	1 (2.1)

Opposite page: Table 1. Stomach contents of Guillemots found in winter. Frequency of occurrence = number of birds in which the respective fish family occurred (in brackets: % of all stomachs). Numerical abundance = total number of items of the respective prey type (in brackets: % of the total number of items).

Tegenoverligende pagina: Tabel 1. Maaginhoud van Zeekoeten die 's winters gevonden zijn. Frequency of occurence = aantal vogels waarin de betreffende visfamilie voorkwam (tussen haakjes % van alle magen). Numerical abundance = totaal aantal items van de betreffende prooi (tussen haakjes % van het totaal aantal items).

Table 2. Stomach contents of Guillemots found in summer. Frequency of occurrence = number of birds in which the respective fish family occurred. Numerical abundance = total number of items of the respective prey type.

Tabel 2. Maaginhoud van Zeekoeten die 's zomers gevonden zijn. Frequency of occurence = aantal vogels waarin de betreffende visfamilie voorkwam. Numerical abundance = totaal aantal items van de betreffende prooi.

Number of stomachs (with food remains)		4 (3)	
Number of prey items (identified)		14 (13)	
		Frequency of occurrence	Numerical abundance
Fishes			
Ammodytidae	*Ammodytes* spec. a/o *Hyperoplus spec.* (Sandeel)	1	6
Clupeidae	*Clupea harengus* (Herring) / *Sprattus sprattus* (Sprat)	2	5
Callionymidae	*Callionymus* spec. (Dragonet)	1	1
Unidentified			1
Invertebrates			
Cephalopoda		1	1

Diet composition in the winter 2001/2002 Remains of five different fish families occurred in the nine stomachs (Table 1). Clupeids and sandeels dominated with a numerical abundance of 64 % and 21 %, respectively. A goby, a three-spined stickleback and a dragonet each were only found once. The samples contained one invertebrate (a tiny gastropod) but no plants.

Diet composition in summer The stomachs contained remains of 13 identifiable prey items, 12 fishes and one cephalopod. Excepting one dragonet *Callionymus* spec., only sandeels and clupeids were found (Table 2). Two stomachs contained plant material. A comparison between the two summer periods was not made because of the small sample size.

Table 3. Fish lengths of sandeels and clupeids in summer. Calculations according to Härkönen (1986).
Tabel 3. Lengte van zandspiering en clupeiden in de zomer. Berekend volgens Härkönen (1986).

	Otolith length (OL) / otolith width (OW) [mm] (corrected for 5 % wear)	Estimated total fish length (TL) [mm]
Sandeel	1.67	96
TL = 8.776 + 51.906 * OL	2.14	120
	1.23	72
	1.90	107
	1.50	86
	0.98	60
Herring	0.91	80
TL = -87.49 + 184.39 * OW	0.99	95
	0.84	67
Sprat	1.05	119
TL = -25.28 + 137.24 * OW		

Fish length in summer Total length (TL) of sandeels ranged from 60 to 120 mm, with a mean of 90 mm. Clupeids averaged 90 mm with minimal and maximal lengths of 67 and 119 mm, respectively (Table 3).

The effect of oiling on diet composition There was no significant difference in the total number of prey found in oiled and unoiled birds from winter 2000/2001 ($G = 3.38$, $P > 0.05$). However, there were some differences between the four main prey families: While clupeids were equally distributed over the stomachs of both categories ($G = 2.41$; $P > 0.10$), sandeels and gobies occurred more frequently in oiled birds ($G = 16.45$ for sandeels, $G = 46.59$ for gobies; $P < 0.001$, respectively). In contrast, there was a higher number of pipefishes in unoiled birds ($G = 117.43$; $P < 0.001$).

DISCUSSION

Limitations on the interpretation of data Studies of stomach contents by dissection of the alimentary tract, especially of birds found dead, are seriously biased towards greater or harder items like otoliths, squid beaks or jaws of polychaete worms (for a review see Duffy & Jackson 1986 and Camphuysen 1990a). Differential digestion and breakdown rates of otoliths from different fish species should be considered (Duffy & Jackson 1986), but adequate data are too scarce (e.g. Cherubini & Mantovani 1997, Leopold & Winter 1997). However, the dominance of rather small otoliths (sandeel, clupeids, gobies) and very small otoliths of pipefishes in this study indicates that this bias was small and the results are likely to be reliable.

Nevertheless, any diet study on dead birds must be considered with caution. Oiled or ill birds might be restricted in, or prevented from feeding and they might take species that are not their preferred prey but are more easy to catch. Blake (1983) found at Hvaler (Norway) that heavily oiled Guillemots took fewer gobies than less oiled birds. By contrast, gadids occurred more frequently in heavily than in lightly oiled birds. In samples from Sweden, however, these differences were not observed. In the present study sandeels and gobies occurred more frequently in oiled birds, but they are a common prey of Guillemots in winter in some areas (Cramp 1985; Blake 1983; Blake 1984) and the high occurrence probably reflects a preference for these fishes rather than a real effect of oiling. Nothing could be said about the high number of pipefishes in unoiled birds and if oiled birds are less capable to capture them. Pipefishes are a very uncommon prey species of Guillemots that has never been published in other diet studies and thus no comparisons are possible. Hence we assume both our samples from oiled and unoiled birds to be representative.

Food spectrum At Helgoland sandeels (Ammodytidae) and clupeids (Clupeidae) are the only fish families known to be brought to the ledges in the breeding season, for display and to feed the chicks (Leopold *et al.* 1992; Grunsky 1994; Grunsky-Schöneberg 1998). The proportions of the two families vary greatly between and even within years. In June 1990 Leopold *et al.* (1992) found 94.6 % clupeids and 5.4 % sandeels brought to the ledges for display and chicks. Between 1991 and 1994 the proportion of sandeels fed to young varied between 21.8 and 68.6 %, and that of clupeids between 78.1 and 31.4 %. During the incubation period sandeels accounted for 32 to 91 %, clupeids for 9 to 68 % of all fishes used for display (1991-1993 only), during chick rearing these proportions were 21 to 73 % and 27 to 79 %, respectively (Grunsky-Schöneberg 1998). Studies in other colonies provide similar results. E. g. on the Isle of May

(Scotland) the chicks are fed with sandeels and clupeids and to a much lesser extent with saithe *Pollachius virens*, mackerel *Scomber scombrus* and gurnards (Triglidae). 99.6 % of display fishes are sandeels and clupeids (Harris & Wanless 1985). Chicks on Skomer Island and Skokholm (Wales) normally get sprats, but sometimes sandeels dominate their diet (Glutz von Blotzheim & Bauer 1982).

Stomach examinations of **adult** Guillemots in summer are scarce. For birds from the Faeroes and the Shetlands sandeels and clupeids are also an important prey for adult birds during the breeding season (Bradstreet & Brown 1985). Adult Guillemots off north and east Scotland mainly eat sandeels in summer (Blake *et al.* 1985). Sandeels (mostly *Ammodytes marinus*), clupeids (*Clupea harengus*, *Sprattus sprattus*) and gadids (*Merlangus merlangius*, *Trisopterus minutus*, *T. esmarkii*, *Gadus morhua*) dominate in the summer diet of adults off western Scotland, with geographical variations between different samples within the study area (Halley *et al.* 1995). The four summer samples collected at Helgoland contained mainly sandeels and clupeids, too. But we also found a dragonet and a cephalopod, prey species that have never been seen taken to the colony. Additionally, the sandeels and clupeids found in the stomachs on average only measured 90 mm and hence were considerably smaller than the prey carried to the breeding ledges. Sandeels taken to the Helgoland colony ranged from 130 to 200 mm and clupeids from 90 to 150 mm with the bulk being 100 to 140 mm (Leopold *et al.* 1992; Grunsky-Schöneberg 1998), similar to those at the Isle of May, where the majority of sandeels and sprats ranged from 130 to 160 and from 120 to 130 mm, respectively (Harris & Wanless 1985). Camphuysen (2001) examined the stomach content of a single adult breeding Guillemot trapped in a pelagic trawl off the Scottish east coast in summer 2001. He found remains of small sandeels *Ammodytes marinus* with a total length of 55-75 mm and remains of Herring and Norway Pout *Trisopterus esmarckii* of similar size. Only one Herring was larger (TL about 110 mm). During the survey where the dead bird was found, Camphuysen observed auks driving balls of sandeels towards the sea surface that also had a TL of 55 to 75 mm, while flying birds carried fishes apparently longer than 100 mm. However, Guillemots also take larger fishes for self-feeding if they are available. Halley *et al.* (1995) found in birds sampled off western Scotland in April and June sandeels with a range from 64 to 228 mm. Fish lengths of sandeels found as predominant prey of Guillemots sampled in April and May in The Netherlands ranged from 60 to 200 mm with the bulk being 140-160 mm (Camphuysen 1990b). These results confirm our assumptions that Guillemots are opportunistic feeders and that the food consumed by adult Guillemots at sea may differ from that provided to the chicks and used for display. Mehlum (2001) observed a difference between the diet of adult Common and Brünnich's Guillemots *Uria*

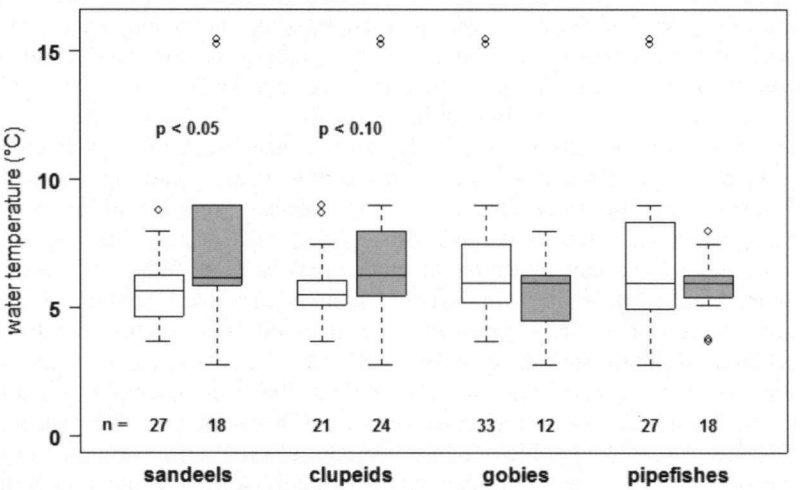

Figure. 1. Water temperatures on the day before sampling of Guillemots containing (grey) and lacking (white) the respective prey groups. (p according to Mann-Whitney-U Test; n = number of birds). Data from both winter periods combined.

Figuur 1. Watertemperatuur op de dag voordat Zeekoeten verzameld werden, met (grijs) en zonder (wit) de respectievelijke prooidiergroepen. (p volgens Mann-Whitney-U Test; n = aantal vogels). Gegevens van beide wnters zijn samengevoegd.

lomvia and chicks in the Barents Sea. While the chicks were fed with fishes the predominant prey of adults were euphausiids. Differences in the diet between adults and chicks are not only found in Guillemots, that can carry only a single fish at high energetic flight costs, but also e.g. in gulls (Ehlert 1971, Spaans 1971, Vermeer 1982, Nogales *et al.* 1995, Dierschke & Hüppop 2003), terns (Glutz von Blotzheim & Bauer 1982) and skuas (Furness 1987), all being much more efficient flyers.

The analysis of the 49 stomachs of both adult and immature birds, found in winter confirmed that the main food of Guillemots around Helgoland is fish. Invertebrates occurred only in very small quantities. With the exception of the Nereid worms they measured only a few millimetres and thus probably originated from the stomachs of prey fish. Blake (1983) found invertebrates,

mainly polychaete worms, in only one percent of 425 dissected stomachs of Guillemots from Hvaler (Norway), in none of 153 stomachs from birds found in Bohüslan (Sweden) and in 11 % of 106 stomachs from birds of Aust-Adger (Norway). In the Pacific, however, squid, euphausiids and amphipods comprise a more important part of the Guillemot diet (Gaston & Jones 1998). In the Barents Sea, crustaceans may be an important prey in years when schooling fishes are not abundant (Mehlum 2001).

In winter 2000/2001 a relatively large number of different fish species were taken as prey. Beside sandeels and clupeids, many gobies and pipefishes and some hooknoses and three-spined sticklebacks were identified and in addition singletons of several other fish species. Gobies have been found to become more important in winter in other areas as well: While on Fair Isle (Scotland) only few gobies are taken in summer they play, beside sprat and gadids, an important part in the winter diet (Cramp 1985). Gobies dominated, together with gadids and clupeids, the diet of Guillemots killed during an oil incident in the Skagerrak in January 1981 (Blake 1983) and were also present in birds off north and east Scotland (Blake *et al.* 1985). However, Durinck *et al.* (1991) found only few gobies in the stomachs of Guillemots drowned in the Skagerrak in winter 1988. In that study clupeids were the most important species, followed by gadids. Clupeids, sandeels and gadids were the most common prey species of Guillemots collected during the mass death of auks on the North Sea coasts of England and Scotland in February 1983 (Blake 1984). The diet of birds washed ashore in The Netherlands in November 1990 (Camphuysen and Keijl 1994), in December 1991 (Camphuysen 1995b) and in February 1992 (Leopold & Camphuysen 1992) comprised mainly clupeids, sandeels and gadids with small quantities of other fish species, for example gobies and dragonets. Sprats and few sandeels and gadids were found in stomachs of Guillemots drowned in the Baltic Sea (Lyngs & Durinck 1998). Sticklebacks in the winter diet of Guillemots were recorded from the Danish coast of the Baltic Sea (Glutz von Blotzheim & Bauer 1982) and from birds stranded on the Dutch coast (Leopold, pers. comm.; Camphuysen and Keijl 1994). Although we found a large amount of pipefishes in our samples from Helgoland, there are no published reports on pipefishes in other studies on Guillemot diet. However, they were found as prey of e.g. Common Gulls *Larus canus* (Reijnders & Keijl 1997) and Kittiwakes *Rissa tridactyla* (Vauk & Jokele 1975).

Beside animal remains some components of plants were found in the stomachs but they are not considered to be a part of the Guillemot diet. They might be taken together with prey fishes captured in the seaweed zone, like pipefishes and gobies. At least one of these species was found in 8 out of 10 stomachs that contained plant material. Similarly, in only 2 % of the stomachs

of Guillemots from the Murmansk coast plant material was found (Bradstreet & Brown 1985), and Glutz von Blotzheim & Bauer (1982) mention only vestiges of plants in the stomachs of birds from Shetland.

The diversity of fishes was much smaller in winter 2001/2002. Beside the dominating sandeels and clupeids only three other species were found. Although the sample size was much smaller in that year, this might reflect interannual differences in the availability of sandeels and clupeids and the high flexibility of adult Guillemots in reacting to changes in the availability of different prey species (Croll 1990). The abundance of sandeels and clupeids might be related to the water temperature: when sandeels and clupeids occurred in the stomachs water temperatures on the day before collecting the dead Guillemots were significantly higher than in absence of these prey families (U-Test: $P < 0.05$ for sandeels, $P < 0.1$ for clupeids; Figure 1). The mean and minimal water temperatures in winter 2001/2002 were 0.6 and 1.5 °C, respectively, higher than in the winter 2000/2001. (Source: Germany's National Meteorological Service „Deutscher Wetterdienst (DWD)", Station Helgoland). Additionally, most clupeids from the second winter were found in stomachs collected in October and only few samples originate from periods with low water temperatures, which might explain the high abundance of this species. For gobies and pipefishes no relationship was found between their presence in the stomachs and water temperature (U-Test: $P < 0.6$ for gobies, $P > 0.9$ for pipefishes). The stomach examinations carried out by Halley *et al.* (1995) also showed a seasonal variation in the prey spectrum. Sandeels dominated in April and June but were absent in August and November, when prey consisted mainly of various clupeids and gadids. No data are available on the seasonal occurrence of prey fishes around Helgoland and more studies are necessary to examine the effect of season and/or water temperature on the availability of different fish species.

Conclusions The diet of Guillemots around Helgoland is dominated by fish throughout the year. In winter, adult and immature Guillemots use a variable prey spectrum with a high proportion of sandeels, clupeids, pipefishes and gobies, probably depending on the availability of the different species. In summer the prey spectrum is smaller and there appears to be a difference between prey for self-feeding of adult Guillemots and prey provided to mates and offspring. This is consistent with Central Place Foraging Theory which predicts that parents should maximize the delivery rate to the colony, particularly if the distance between feeding ground and colony is large and costs for transport are high (Orians & Pearson 1979). Guillemots are poor flyers that can carry only a single fish at a time. Therefore it is more efficient to deliver only prey items of high energetic value to the colony. Additionally, foraging

Guillemots are exposed to kleptoparasitism from Kittiwakes and larger *Larus* gulls in summer (own observations by O. Hüppop) and should therefore carry only fishes to the colony if their size and calorific value are "worth the risk". For self-feeding, also smaller or lower quality fishes, unacceptable for transport to the colony, are sufficient for the more opportunistic adult Guillemots.

ACKNOWLEDGEMENTS

We are grateful to Malte Seehausen, Verein Jordsand, for the collection of Guillemot corpses at Helgoland in winter 2000/2001 and to the team of the Station for the collection of dead birds in summer months and in winter 2001/2002. Dr. D. Keyser, University of Hamburg, kindly took photos of fish otoliths with the SEM. Special thanks to Mardik Leopold for making most valuable suggestions to the manuscript.

SNACKS UIT DE DIEPTE: ZOMER- EN WINTERDIEET VAN ZEEKOETEN *URIA AALGE* ROND HELGOLAND

Maaginhouden van 53 aangespoelde Zeekoeten op het eiland Helgoland in de zuidoostelijke Noordzee werden onderzocht op prooiresten. In de winter 2000/2001 was het voedselspectrum divers. Er werden resten gevonden van soorten behorend tot tien verschillende families van beenvissen, met zeenaalden, grondels, zandsprieringen en haringachtigen als meest voorkomende prooien. Ongewervelden droegen slechts 1% bij aan alle prooien. De diversiteit was in de winter van 2001/2002 aanzienlijk lager, waarbij haringachtigen en zandspiering kwantitatief de hoogste abundantie hadden, en er slechts drie andere families werden gevonden (tabel 1). De aantallen zandspiering en haringachtigen zijn mogelijk gerelateerd aan de watertemperatuur. Indien deze visfamilies aanwezig waren in de magen, was de watertemperatuur de dag voordat de dode Zeekoeten verzameld waren hoger dan wanneer deze soorten afwezig waren (fig 1). Het geringe aantal monsters dat in de zomer werd verzameld bevatte met name zandspiering en haringachtigen (tabel 2), soorten die ook naar de kolonie worden gebracht voor de balts en voor het voeden van de kuikens. De vissen die in de magen van adulte vogels werden gevonden, waren echter kleiner dan de vissen die naar de broedrichels werden gebracht. Bovendien werden een pitvis en een inktvisachtige in de magen gevonden; prooien die nooit in de kolonie vastgesteld zijn. Dit bevestigt ons vermoeden dat waarnemingen van soorten die naar de kolonie worden gebracht, niet representatief zijn voor het dieet van volwassen vogels. Deze voeden de kuikens met relatief grote vissen met een hoge voedingswaarde. Als ze zelf foerageren, zijn ze opportunistischer en consumeren ze kleinere en magerder prooien. Dit is in overeenstemming met de voedseltheorie.
Tekortkomingen van de gebruikte methoden en het effect van oliebesmeuring worden bediscussieerd. Terwijl olie geen invloed op het totaal aantal prooien in de maag van dode Zeekoeten lijkt te hebben, vonden we in de magen van olievogels vaker zandspieringen en grondels, en vaker zeenaalden in de magen van niet met olie besmeurde vogels.

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