CRUSTACEANS IN THE DIET OF ADULT COMMON AND BRÜNNICH'S GUILLEMOTS *URIA AALGE* AND *U. LOMVIA* IN THE BARENTS SEA DURING THE BREEDING PERIOD

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SUMMARY

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The diet of adult Common and Brünnich's Guillemots *Uria aalge* and *U. lomvia* during the breeding season was studied from birds collected at sea near Bear Island in the central Barents Sea. In both species the euphausiid *Thysanoessa inermis* was the predominant prey. Euphausiids have not previously been reported as a major component of the diet of adult Common Guillemots in the Atlantic. Previous studies at the colonies of Bear Island have shown that fish, mostly Capelin *Mallotus villosus*, are the main prey fed to chicks. Optimal foraging theory predicts that guillemots, as single-prey loaders foraging out at sea, would maximise the rate of energy provided to the chicks by selecting large and high-quality prey such as Capelin. I argue that self-feeding on euphausiids in years with low fish abundance may be an important strategy for guillemots in regions where the availability of schooling fishes fluctuates unpredictably.

Key words: Common Guillemot, *Uria aalge*, Brünnich's Guillemot, *Uria lomvia*, murres, Barents Sea, diet, Capelin, euphausiids

INTRODUCTION

The literature on the diet of adult Common Guillemots *Uria aalge* during the breeding season states that schooling pelagic fish species are their most important prey (see review by Gaston & Jones 1998). Large pelagic zooplankton, such as euphausiids and amphipods, are reported as components of the adult diet in some regions, but in comparative studies of Common and Brünnich's Guillemots *U. lomvia* in the same region, the diet of the latter had a higher proportion of crustaceans (Gaston & Jones 1998). In the Barents Sea, there are few studies of the summer diet of adult Common Guillemots (see review by Barrett *et al.* 1997a), but fish also predominate in the diet in previous studies from this region. In the Barents Sea both of these guillemot species breed in mixed colonies, which allows a comparative study of their diets.

Both Common and Brünnich's Guillemots feed their chicks almost entirely on fish, usually a single species of schooling fish (Bradstreet & Brown 1985, Gaston & Jones 1998). However, in years with low abundance of schooling fishes, other prey such as squid or benthic fishes may constitute important parts of the chick diet (Barrett *et al.* 1997a,b). In the central Barents Sea, south of the Polar Front, Capelin *Mallotus villosus* is the major schooling fish prey available to breeding seabirds. This species is the main fish in the diet of guillemot chicks at colonies to the south (northern Norway) and at Bear Island (Barrett *et al.* 1997a,b). The Capelin stock in the Barents Sea is subject to large fluctuations (Gjøsæter *et al.* 1998), and in some years it may not be large enough for the subsistence of the guillemot populations residing in the area. Thus, the guillemots are likely to switch to other prey in years with low Capelin abundance. A similar change in diet in years with low abundance of Capelin has been reported from Alaska (Baird 1991), when adult Tufted Puffins *Fratercula cirrhata* consumed more invertebrate prey than in other years, although chicks were still mainly fed fish.

In this paper, I compare the diet of adult Common and Brünnich's Guillemots near Bear Island during the breeding season in a year when Capelin abundance in the Barents Sea was low. I discuss the results in relation to chick diet and central place foraging theory (Orians & Pearson 1979).

MATERIAL AND METHODS

Bear Island (74°30'N, 19°01'E) supports some of the largest seabird colonies in the Barents Sea region. Common and Brünnich's Guillemots are the two most abundant alcid species breeding on the island. The populations of these species combined were estimated in 1986 at 350 000 breeding pairs (Mehlum & Bakken 1994).

Physical oceanography near Bear Island is characterised by non-stratified, relatively cold water close to the island, surrounded to

the south and west by a frontal region (the Polar Front) where this water mass mixes with warm Atlantic water. The location of this front is relatively stable and generally follows the 100-m isobath near the island (Johannessen & Foster 1978, Mehlum *et al*. 1998). A strong tidal current mixes the whole water column in shallow waters around the island, whereas the water is horizontally stratified on the deep-water side of the surface expression of the front (Mehlum *et al*. 1998). Such frontal areas with strongly stratified water are known to aggregate seabird prey and are important foraging areas for seabirds (Kinder *et al*. 1983, Schneider *et al*. 1990, Coyle *et al*. 1992, Decker & Hunt 1996, Mehlum *et al*. 1998).

Totals of 26 Common Guillemots and 38 Brünnich's Guillemots were shot from a small boat on 3–5 July 1996 near the Polar Front at distances 5–72 km south and south-east of Bear Island. Birds were collected from groups of individuals that were thought to be actively foraging. The sampling area was within the normal foraging range of guillemots breeding at Bear Island (Mehlum *et al*. 1998). The sample was obtained in the early chick-rearing period. Guillemots of both species were frequently observed flying towards the colony and carrying fish in their bills. Stomach and oesophagus contents of the birds were placed in a deep freezer within an hour after collection, and later identified to the lowest possible taxon. Two fish otoliths from the same stomach, differing by less than 0.5 mm in length, were considered to be from the same fish. Unidentified, partly digested fish were identified to species using the otoliths in their respective sample, provided that the fish's length was similar to that estimated from otolith length. Abdomen length was measured in whole specimens of the euphausiid *Thysanoessa inermis*, and divided by a factor of 0.94 to obtain total length (J.M. Weslawski pers. comm.). The ages of the *T. inermis* specimens were estimated based on total length according to Dalpadado & Ikeda (1989).

I used frequency of occurrence and numerical abundance of different prey taxa in the analysis of the diet (Duffy & Jackson 1986). *Frequency of occurrence* was determined as the percentage of sampled birds in which the prey type occurred. *Numerical abundance* was defined as the percentage by number of a prey type compared to the total number of identified prey items from all stomachs combined.

RESULTS

All birds sampled except one Brünnich's Guillemot contained identifiable food remains. The diet of Common Guillemots, in which only five taxa were identified, was less diverse than that of Brünnich's Guillemots (nine taxa identified, Table 1). Euphausiids *Thysanoessa* spp. were the predominant prey both in terms of numerical abundance and frequency of occurrence in Common Guillemot as well as in Brünnich's Guillemot. They accounted for 98% and 99% of the number of prey items recorded in the two species, respectively, and were found in 81% of all Common Guillemots sampled and in all Brünnich's Guillemots that contained prey remains. Of those specimens identified to species level as prey of Common Guillemot, all (26) were *Thysanoessa inermis*. Of the 72 individuals identified to species level in Brünnich's Guillemots, 70 were *T. inermis* and two were *T. raschii*. There was no difference in the sizes of *T. inermis* taken by the two guillemot

TABLE 1

Frequency of occurrence and numerical abundance of prey taxa in 26 Common Guillemots *Uria aalge* and 38 Brünnich's Guillemots *U. lomvia* sampled in the Bear Island region in July 1996

Taxon	Common Guillemot		Brünnich's Guillemot	
	Frequency of occurrence (%)	Numerical abundance (%)	Frequency of occurrence (%)	Numerical abundance (%)
Invertebrates				
Polychaeta sp.	6 (23.1)	17 (1.0)	5 (13.2)	12 (0.3)
Gonatus fabricii	4 (15.4)	10 (0.6)		
Onisimus sp.	1 (3.8)	1 (0.1)		
Gammarus wilkitzkii			2 (5.3)	2 (0.0)
Themisto libellula			4 (10.5)	13 (0.3)
Thysanoessa sp.	21 (80.8)	1753 (98.0)	37 (97.4)	4180 (98.9)
Lebbeus polaris			1 (2.6)	2 (0.0)
Spirontocaris spinus			1 (2.6)	2 (0.0)
Fishes				
Boreogadus saida			3 (7.9)	5 (0.1)
Liparis sp.			1 (2.6)	2 (0.0)
Myoxocephalus sp.			1 (2.6)	1 (0.0)
fish, unidentified	7 (26.9)	7 (0.4)	6 (15.8)	6 (0.1)
Total	**–**	**1788**	**–**	**4213**

species (Mann-Whitney U-test, $z = -0.940$, $P = 0.35$). The total length averaged 23.3 mm (range 20–29 mm).

Fish were present in 27% of the Common Guillemot samples, but no species were identifiable. No Capelin was positively identified in any sample, but Polar Cod *Boreogadus saida* (five individuals) was encountered in three Brünnich's Guillemots. Two species of benthic fishes and two species of shrimp were also encountered in Brünnich's Guillemots. Polychaetes and the squid *Gonatus fabricii* occurred frequently in Common Guillemots, but only polychaetes were present in Brünnich's Guillemots. The pelagic amphipod *Themisto libellula* was present in more than 10% of the Brünnich's Guillemots but in none of the Common Guillemots. One specimen of an amphipod *Onisimus* sp. was encountered in a Common Guillemot and two specimens of the amphipod *Gammarus wilkitskii* were found in Brünnich's Guillemots.

DISCUSSION

This study from Bear Island showed that, at least in some years and in parts of the breeding season, the diets of adult Common and Brünnich's Guillemots comprise mainly euphausiids. A high predominance of euphausiids was also recorded in adult Brünnich's Guillemots sampled at sea near Bear Island in 1993 (Mehlum *et al*. 1998). However, the present study is the first to document the diet of adult Common Guillemots during the breeding season in the central Barents Sea. The predominance of euphausiids in Common Guillemots contrasts with the results of previous studies in the Barents Sea region (Barrett *et al*. 1997a) and elsewhere in the Atlantic (Bradstreet & Brown 1985, Gaston & Jones 1998).

In the five years studied by Barrett *et al*. (1997b) crustaceans were not observed among prey fed to chicks of Common and Brünnich's Guillemots at Bear Island. Their study comprised both years with low and high Capelin abundance in the Barents Sea (Gjøsæter *et al*. 1998). Little information was obtained on the diet of guillemot chicks at Bear Island in 1996. Eight meals delivered to Brünnich's Guillemot chicks concurrent with the present study consisted of fish, of which one was a Capelin (V. Bakken pers. comm.). The observations from Bear Island indicate that there is a dichotomy in the self-feeding and provisioning diet of both species of guillemot at Bear Island. However, further studies are needed in order to verify this observation.

Guillemots are single-prey loaders and carry the food in their bill back to their chicks. Being central place foragers (Orians & Pearson 1979) they have to spend energy to transport the prey from the foraging area at sea to the breeding colony. It would thus be most efficient to select a relatively large and high-quality fish to bring back to the chick. If a smaller, suitable prey is abundant in the foraging area, it may be a more efficient strategy for the adult to self-feed on this smaller prey and select a large prey item for provisioning the chick. This dichotomy is consistent with optimal foraging strategy (MacArthur & Pianka 1966, Charnov 1976, Stephens & Krebs 1986, Houston 1987, Ydenberg 1994). As predicted by theory, several studies have shown that when self-feeding, alcids take smaller or lower-quality prey than that provisioned to the chicks (Bradstreet & Brown 1985, Vermeer *et al*. 1987, Baird 1991, Davoren & Burger 1999).

The area near the Polar Front south and east of Bear Island is a major spawning ground in the Barents Sea for the euphausiid *T. inermis* (Lofnes 1993), and the majority of the spawning individuals are two years and older (Dalpadado & Skjoldal 1991, 1996). The size of the euphausiids in the diet of the guillemots indicated that they were adult individuals (two years and older). The euphausiids are probably easily accessible to the guillemots in this area and therefore a preferred prey.

The euphausiid *T. inermis* is of high energetic value (24.3–26.0 $kJ.g^{-1}$ dry mass (Percy & Fife 1981); 25.1 $kJ.g^{-1}$ dry mass (Weslawski & Kwasniewski 1990)), but Capelin fed to guillemot chicks in Labrador was reported to be even higher in energy content, 28.3 $kJ.g^{-1}$ dry mass (Birkhead & Nettleship 1987). Guillemots might select euphausiids as self-feeding prey because they are found in higher abundance and are more easily obtainable than schooling fishes. Thus, by self-feeding on dense swarms of euphausiids, the guillemots will obtain a higher rate of energy while foraging. No data are available on Capelin abundance in the study area during the summer of 1996. However, in that year the Capelin stock size in the whole Barents Sea was very low (0.3 million tonnes) compared to years with large stock size (>4 million tonnes) (Gjøsæter *et al*. 1998).

The predominance of crustaceans in the adult diet recorded in both species of guillemot at Bear Island is probably a feature that is more common than previously thought in regions where large aggregations of schooling fishes are not available as the predominant prey every year. In the Barents Sea, the distributions of Capelin and the euphausiid *Thysanoessa inermis* overlap, and *T. inermis* is an important prey for Capelin (Ajiad & Pushchaeva 1992). An inverse relationship has been documented between the abundance of Capelin and *T. inermis* in the Barents Sea (Dalpadado & Skjoldal 1995, 1996). In years when Capelin are scarce, the guillemots may rely more on euphausiids for self-feeding. No data are available to verify whether the guillemots feeding in the Bear Island area change their self-feeding diet between years as a response to prey availability. If they do, prey switching may function as a buffer in a system where schooling fish stocks may fluctuate unpredictably.

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