Winter Diet of Atlantic Puffins (*Fratercula arctica*) in the Northeast Atlantic

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Abstract.—Stomach contents were analyzed from Atlantic Puffins (*Fratercula arctica*) killed during winter near the Faroe Islands, Denmark (N=25), or in the Norwegian Sea 296-740 km to the north (N=11). The diet of the birds in the two areas were strikingly different. Offshore, puffins fed almost exclusively on the Glacier Lantern Fish (*Benthosema glaciale*) and on squid (*Gonatus fabricii*). In shelf waters around the Faroes, the diet was dominated by euphausiid crustaceans (mainly *Thysanoessa inermis*) and a variety of fish species (*Ammodytes* sp., *Mallotus villosus*, and others). Polychaete worms were present in small numbers in both samples. The results confirm that invertebrates may play a significant role in the diet of adult puffins; however, a rough estimate indicated that on a mass basis, fish (ranging in length from 4 to 14 cm) were the most important prey type in both the samples examined. *Received 18 February 1992, accepted 29 July 1992.*
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Like most other seabirds, the Atlantic Puffin (*Fratercula arctica*) has been much more thoroughly studied during the breeding season than in other parts of the year. This bias is particularly evident in case of the feeding ecology. Chick diet (almost exclusively small fish) has been studied at a number of colonies, as summarized by Bradstreet and Brown (1985).

These authors also reviewed the more fragmentary data on the summer diet of adult puffins (mainly fish but with varying amounts of crustaceans and polychaetes) but concluded that "nothing is known of the diet of Atlantic Puffins in winter" (Bradstreet and Brown 1985, p. 294) when they have a more dispersed and pelagic distribution than other alcid species (Brown 1985).

Puffins are present in coastal Faroese waters and offshore parts of the Northeast Atlantic during winter (Jensen 1986), when small numbers are shot or accidentally caught on baited long-lines set for Salmon (*Salmo salar*). In this paper, we present an analysis of the winter diet of Atlantic Puffins killed in coastal Faroese waters and in pelagic fishing areas in the Northeast Atlantic. The objective is to determine the winter diet of the puffins in relation to location (coastal vs. pelagic), and thereby increase our understanding of this seabird species while at sea, where it spends most of its life but is difficult to study.

MATERIALS AND METHODS

A total of 36 puffins killed during January, February and March 1987 and 1988 were obtained from hunters and fishermen. Twenty one of the birds (14 adults and 7 immatures) were collected (shot or caught) in the shelf area within 20 km of the Faroe Islands, Denmark. The remaining 15 (11 adults and 4 immatures) were caught outside the 2000 m isobath in the Norwegian Sea, 296-740 km (160-400 nautical miles) north of the Faroes (Fig. 1) on salmon long-lines baited with Sprat (*Sprattus sprattus*). As no Sprats were detected in the stomachs, the long-line bait has not biased the data.

The birds were aged by the development of the bill-grooves (Petersen 1976) and, in data analyses, birds were grouped as 'immature' (1st - 4th calendar year) or 'adults'. During dissection, the birds were sexed and the stomachs were removed, slit and stored in 96% ethanol until examination. Also, wing length (maximum flattened wing) of most specimens was measured in order to get a clue to the origin of the wintering populations (cf. Jensen 1986, Harris *et al.* 1991).

Stomach contents were washed into a tray, taking care that no small objects such as fish otoliths remained in the gizzard. Prey remains were sorted by taxon, partly digested crustaceans usually to the order level, while the few intact specimens of crustaceans and most fish were determined to genus or species level using standard reference keys and otolith guides (Enckell 1980, Breiby 1985, Härkönen 1986). Broken individuals of euphausiids were counted by the number of pairs of eyes, and amphipods by tail parts. Samples of intact crustaceans were measured to the nearest mm from the eyes to the tip of the telson.

We counted the number of squids by the greater number of upper or lower beaks, and we used the number of paired jaws of similar size for polychaete worms. Fish were mainly represented by otoliths and

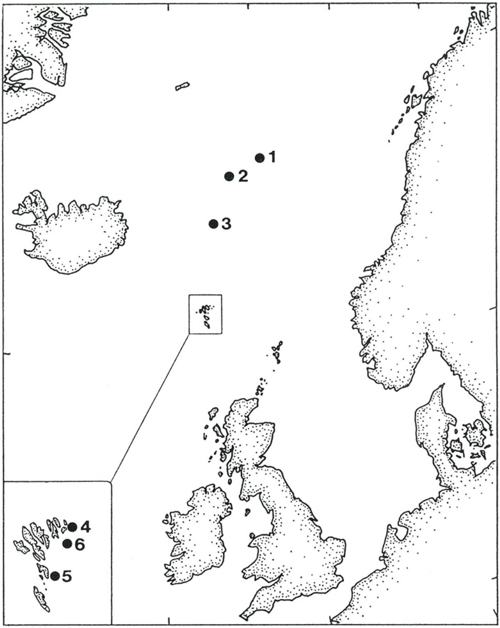

Figure 1. Sampling locations for Atlantic Puffins included in analysis of winter diet. Locations 1-3 are pooled as 'offshore' samples in the Norwegian Sea and 4-6 as 'coastal', i.e. the shelf area near the Faroe Islands.

the presence of spines and bone fragments. Otoliths were measured with calipers to the nearest 0.1 mm. Following Bradstreet (1980) we assumed that one fish had been eaten if the length of two otoliths differed by less than 0.2 mm, otherwise we assumed that the otoliths originated from two different fishes. The size of ingested fishes was subsequently estimated from regressions of fish length on otolith length or width (Breiby 1985, Härkönen 1986).

Many otoliths were broken and almost all crustaceans were in an advanced state of digestion. Therefore, although the number of individuals ('numerical abundance', cf. Duffy and Jackson 1986) and frequency of occurrence could be determined, the size of prey could only be assessed for a fraction of the total number of food items. Apart from the general considerations in the Discussion, we made no attempt to estimate wet mass or caloric contributions to the diet by each taxon because sampling methods did not allow such definite treatments. Sample size, though, may be sufficient to warrant non-parametric two-sample tests (Duffy and Jackson 1986) and, to detect dietary differences, we compared the relative numerical abundance (percentage by numbers) of fish versus invertebrates by Wilcoxon rank sum test (two-tailed). Differences in the sizes of fish eaten were tested by Student's t-test. One stomach contained no prey remains and was excluded from the data analysis.

RESULTS

General trends

A total of 1570 food items were recorded in the 35 stomachs containing prey remains. In terms of frequency of occurrence, invertebrates and fish were equally common, being present in 94% and 89%, respectively, of the stomachs (Table 1). Crustaceans numerically dominated the diet. Euphausiids were especially abundant and made up 82% of all prey items. Polychaete worms and squid accounted for 5% and 2%, respectively, of all recorded food items.

The relative numerical abundance of fish versus invertebrates did not differ significantly between years, sexes or age classes and data were subsequently pooled.

Prey species

Unidentified sandlances (*Ammodytes* spp.) were the most common fish species followed by Glacier Lantern Fish (*Benthosema glaciale*) and Capelin (*Mallotus villosus*) (Table 1). Among the items pooled as 'Other fish' in Table 1 was one Norway Pout (*Trisopterus esmarkii*) and one eelpout, probably Vahl's Eelpout (*Lycodes vahli*); the remaining were small specimens of unidentified gadoids. All 32 euphausiids (from 11 stomachs) identified to species were *Thysanoessa inermis*; however, one unidentified individual was of another species. Among 20 amphipods from eight stomachs were two *Hyperia galba*, 10 *Parathemisto gaudichaudi* and one *P. abyssorum*, while the remaining seven specimens probably also belonged to this latter species. All intact squid beaks derived from *Gonatus fabricii*, and the broken beaks likely did as well (T. Kristensen 1990, pers. comm.). The polychaete worms were almost certainly *Nereis pelagica* (J. B. Kirkegaard 1990, pers. comm.).

Even though the sample size is small, it revealed a striking difference in the diet in puffins sampled in offshore areas versus birds from the shelf area near the Faroe Islands: all Glacier Lantern Fish and most squid occurred in the birds sampled in offshore waters — both taxa were found

Table 1. Sampling location, numbers (n), proportion by numbers (%) and frequency of occurrence of major taxa in the winter diet of Atlantic Puffins.

		Sampling zone								
	Sampling location[1]	Offshore (N=14)			Coastal (N=21)			Total (N=35)		
		n	%	FO%[2]	n	%	FO%[2]	n	%	FO%[2]
Ammodytes sp.	3,4,5,6	1	2	7	45	3	71	46	3	46
Benthosema glaciale	1,2,3	22	37	71	0	0	0	22	1	29
Mallotus villosus	2,4,6	1	2	7	16	1	24	17	1	17
Other fish	4,6	0	0	0	42	3	33	42	3	20
Amphipods	2,4,5,6	2	3	7	34	2	38	36	2	26
Euphausiids	4,5,6	0	0	0	1293	85	90	1293	82	54
Polychaetes	1,3,4,6	8	13	14	78	5	52	86	5	37
Squid	1,2,3,4,6	26	43	86	5	0	14	31	2	43
Total fish		24	40	86	103	7	90	127	8	89
Total invertebrates		36	60	93	1410	93	95	1446	92	94
Grand total		60	4		1513	96		1573	100	

[1]See Fig. 1 for location codes
[2]FO% = frequency of occurrence

at all three offshore stations (Table 1). All other taxa predominated in the diet of birds feeding in the shelf areas. Euphausiids were only encountered in the coastal samples as were the fish species pooled as 'Other fish' in Table 1. Sandlances, amphipods and euphausiids were recorded at all coastal sampling locations. Overall, the puffin's diet appeared much more diverse in the coastal area than in the offshore area.

The estimated size of individual fishes ranged from 38 mm (a Glacier Lantern Fish) to 144 mm (a sandlance). On average, the pelagic Glacier Lantern Fish was also the smallest fish species taken (mean 57.1 mm), and the sandlances the largest (mean 104.9, Table 2). The sizes of fish eaten did not differ significantly ($P>0.05$) between years, sexes or age classes.

Origin of birds

There was no significant difference ($t_{19}=-0.91$, $P=0.37$, n.s.) in wing length between immature birds (mean ± s.d., 167.9 mm ± 8.5, n=9) and adult birds (170.7 mm ± 5.5, n=12), but the difference between coastal (166.6 mm ± 7.5, n=11) and offshore birds (172.6 mm ± 4.8, n=10) was significant ($t_{19}=-2.15$, $P=0.04$), suggesting that the puffins sampled in offshore waters derived from colonies farther to the north than did the birds taken in Faroese shelf areas (cf. Jensen 1986, Harris *et al.* 1991).

DISCUSSION

In food studies based on stomach analysis, different digestion rates of various taxa, or of prey items of different size, will inevitably bias the data in favor of the larger and the least digestible items (Bradstreet 1980, Wilson *et al.* 1985, Duffy and Jackson 1986). This is especially so in this study where we have had no influence on the storage condition of the birds until long after death. Therefore, the results of this study may be biased towards the larger prey items.

Previously, the only information on winter diet of the Atlantic Puffin derived from Harris (1984, p. 127), who mentioned that, besides fish, "in the winter, adults also eat numbers of pelagic polychaete worms . . . , pelagic shrimps, gammarids and other crustacea and a few pelagic molluscs," although no details were given. More recently, stomach contents were reported from 64 emaciated puffins washed ashore in Shetland in mid-winter 1990-91. Fish otoliths were found in 15, and polychaete jaws in 5 of the stomachs (Harris *et al.* 1991). The 18 fish otoliths recovered came from *Trisopterus* sp. and unidentified gadids, gobiids and sandlances. As the birds were emaciated and contained very few prey remains, easily digestible items like crustaceans would have little chance of being detected. Our sample is more likely to represent the 'normal' diet.

Table 2. Mean length (mm) of food items in the winter diet of Atlantic Puffins.

Taxon	Mean ± s.d.	n	Regression line[1]
Mallotus villosus	65.6 ± 7.5	15	FL = 14.83 + 45.58 OL
Benthosema glaciale	57.1 ± 9.2	19	FL = -3.31 + 31.79 OW
Trisopterus esmarkii	75.6 ± 8.3	2	FL = -42.6 + 29.522 OL
Lycodes vahli	111.8	1	FL = 21.19 + 37.74 OL
Ammodytes sp.[2]	104.9 ± 13.3	38	FL = 8.776 + 51.906 OL
Hyperia galba	12.0 ± 0	2	
Parathemisto abyssorum	15.0	1	
P. gaudichaudi	16.0 ± 3.5	4	
Thysanoessa inermis	20.8 ± 2.0	11	

[1]Fish length (FL) estimated from regression of otolith length (OL) or otolith width (OW) (all linear measurements in mm). Regressions from Härkönen (1986), except that *Benthosema glaciale* is from Breiby (1985).
[2]Otoliths of sandlance species are very similar; calculation of fish length based on regression of three species, *A. tobianus*, *A. marinus* and *Hyperoplus lanceolatus* (Härkönen 1986).

All of the fish species preyed upon by the 'coastal' birds in this study are known to be taken by puffins in Great Britain during the breeding season (Harris and Hislop 1978), when adult puffins usually forage relatively close to their colonies (Harris 1984, Bradstreet and Brown 1985). The most common fishes recorded in the winter diet, the sandlances, were also the most important prey type brought back to the breeding sites in Great Britain (Harris 1984). In Newfoundland, sandlances were important in the chick diet in a year when the usual food, Capelin, was scarce (Nettleship 1991). The Glacier Lantern Fish, however, is a pelagic species mainly occurring outside the 500 m isobath (Muus 1990). This species, therefore, can mainly be utilized by wintering or non-breeding birds not tied to land. Similarly, the Boreo-Atlantic Gonate Squid (*Gonatus fabricii*) recorded in the winter diet is also mainly found in offshore waters (Kristensen 1984); Harris and Hislop (1978) identified the squid *Alloteuthis subulata* among the few invertebrates brought back to breeding colonies in Great Britain.

In Faroese waters, the Capelin is at the edge of its distribution (Jangaard 1974, Muus 1991) and, therefore, probably not nearly as important for seabirds as is the case in arctic waters (Brown 1985, Nettleship 1991).

The lantern fishes are known to perform daily vertical migrations, being most concentrated in the surface waters during the dark hours (Muus 1990), where they are most accessible to foraging seabirds. This suggests that the puffins may exploit the fish at night or dusk, as is also discussed by Bradstreet and Brown (1985). Vermeer *et al.*(1987) likewise considered the presence of lantern fish species in the diet of Thick-billed Murres (*Uria lomvia*) an indication of foraging at dusk and dawn.

Numerically, the invertebrates were the most abundant prey items in the diet of wintering puffins; however, using numerical abundance to compare importance of taxa of very different size overestimates the significance of small, numerous prey (Duffy and Jackson 1986). In our sample, fish, although far less abundant than the invertebrates, seem to be the most important food in terms of wet mass and energy contents. Although we have not been able to make accurate calculations of wet mass of prey, a rough estimate of the relative importance of fish versus invertebrates can be derived from the mean size of fish otoliths (Härkönen 1986) and from estimates of size-mass relationships of the invertebrate taxa. By treating the unidentified gadoids as Norway Pouts, assigning the Glacier Lantern Fish (no conversion factor to fish mass available, Härkönen 1986) the same mean mass as the longer but slender Capelin, and assigning the crustaceans and nereids a mass of 0.1 g and the squid 1 g (Falk and Durinck, unpubl. data), the proportions of fish and invertebrates by wet mass are estimated as 60% and 40%, respectively. This applies to the pooled sample of puffins. Because most invertebrates were taken in the coastal area, the proportion of fish by biomass may be even higher for the birds feeding in offshore areas, but the proportion was not calculated due to the lack of a conversion factor for the Glacier Lantern Fish.

Sandlances (*Ammodytes* spp.) and other fishes, considered 'high-quality' prey due to the high energy-contents (Harris and Hislop 1978, Vermeer and Devito 1986), are very important prey to seabirds breeding in the northeast Atlantic and appear to contribute to the puffin's winter diet as well. But as the puffins wintering in the shelf area also took many crustaceans, one can speculate that the sandlance stocks accessible to the birds are not able to sustain large numbers of birds during the winter. This may be one reason why many puffins winter in offshore waters where they can take advantage of non-gregarious pelagic prey.

In conclusion, our study specified the qualitative description of the diet of the adult Atlantic Puffin given by Harris (1984), but also detected differences in the diet of puffins feeding in pelagic and shelf areas, respectively, and determined some of the prey species exploited by the birds wintering in the northeast Atlantic.

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Literature Cited

Bradstreet, M. S. W. 1980. Thick-billed murres and black guillemots in the Barrow Strait area, N.W.T., during spring: diets and food availability along ice edges. Canadian Journal of Zoology 58: 2120-2140.

Bradstreet, M. S. W. and R. G. B. Brown. 1985. Feeding ecology of the Atlantic Alcidae. Pp. 263-318. *In*: The Atlantic Alcidae (Nettle ship, D.N. and T.R. Birkhead, Eds.) London, England: Academic Press.

Breiby, A. 1985. Otolitter fra saltvandsfisker i Nord-Norge. Tromura, naturvitenskap nr. 45. Universitetet i Tromsø, Institut tet for museumsvirksomhet, Tromsø Museum.

Brown, R. G. B. 1985. The Atlantic Alcidae at sea. Pp. 383-426. *In*: The Atlantic Alcidae (Nettle ship, D.N. and T.R. Birkhead, Eds.) London, England: Academic Press.

Duffy, D. C. and S. Jackson. 1986. Diet studies of seabirds: a review of methods. Colonial Waterbirds 9: 1-17.

Enckell, P. H. 1980. Kräftdjur. Lund, Sweden: Signum.

Harris, M. P. 1984. The Puffin. Calton, England: T. and A.D. Poyser.

Harris, M. P., M. Heubeck, and D. Suddaby. 1991. Results of an examination of Puffins *Fratercula arctica* washed ashore in Shetland in winter 1990-91. Seabird 13: 62-66.

Harris, M. P. and J. R. G. Hislop. 1978. The food of young Puffins *Fratercula arctica*. Journal of Zoology, London 185: 213-236.

Härkönen, T. 1986. Guide to the otoliths of the bony fishes of the Northeast Atlantic. Copenhagen, Denmark: Danbiu.

Jangaard, P. M. 1974. The Capelin (*Mallotus villosus*): biology, distribution, exploitation, utilisation, and composition. Fisheries Research Board of Canada Bulletin 186: 1-70.

Jensen, J.-K. 1986. [The origin of Puffins wintering in Faeroese waters]. Dansk Ornitologisk Forenings Tidsskrift 80: 131-132 (in Danish with English summary.)

Kristensen, T. K. 1984. Biology of the squid *Gonatus fabricii* (Lichtenstein, 1818) from West Greenland waters. Meddelelser om Grønland, BioScience 13: 3-20.

Muus, B. 1990. Fisk. *In:* Grønlands Fauna (Muus, B., F. Salomonsen and C. Vibe, eds.). Copenhagen, Denmark: Gyldendal.

Nettleship, D. N. 1991. The diet of Atlantic Puffin chicks in Newfoundland before and after the initiation of an international Capelin fishery, 1967-1984. Pp. 2263-2271. *In*: Acta XX Congressus Internationalis Ornithologici.

Petersen, A. 1976. Size variables in Puffins *Fratercula arctica* from Iceland, and bill features as criteria of age. Ornis Scandinavica 7: 185-192.

Vermeer, K. and K. Devito 1986. Size, caloric content, and association of prey fishes in meals of nestling Rhinoceros Auklets. The Murrelet 67:1-9.

Vermeer, K., S. G. Sealy, and G. A. Sanger. 1987. Feeding ecology of Alcidae in the eastern North Pacific Ocean. Pp. 189-227. *In*: Seabirds: Feeding Ecology and Role in Marine Ecosystems (J.P. Croxall, Ed.) Cambridge, England: Cambridge University Press.

Wilson, R. P., G. D. La Cock, M. -P. Wilson, and F. Mollagee 1985. Differential digestion of fish and squid in Jackass Penguins *Spheniscus demersus*. Ornis Scandinavica 16: 77-79.