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The winter diet of the Atlantic Puffin *Fratercula arctica* around the Faroe Islands

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Most mortality of Puffins occurs outside the breeding season but little is known about the species' diet at that time. The stomach contents of 176 Puffins shot legally for food around the Faroe Islands between October and January in three winters were examined. The remains of 20 species of fish, six species of crustacea and single species of polychaete, chaetognathid and squid were identified. The most frequently recorded prey in terms of frequency of occurrence were 0 group (less than one year old) Lesser Sandeel *Ammodytes marinus* (82% of stomachs), followed by mesopelagic fish (52%), nereid worms (41%), Silver Rockling *Gaidropsarus argentatus* (36%), crustacea (35%), large sandeel (32%) and other large fish (32%). In terms of calculated biomass, nereids (41%), large sandeel (23%) and other large fish (17%) made up the bulk of the diet but the latter two prey types were most important in energetic terms (46% despite accounting for only 9% of items). Stomachs contents collected on the same day and location were significantly more similar than those collected on different dates and locations, suggesting that during winter Puffins are generalists taking any prey they encounter.

Keywords: sandeel, diet analysis, polychaete worms, meospelagic fish, Northeast Atlantic, prey consumption

The Atlantic Puffin *Fratercula arctica* is one of the commonest seabirds in the North Atlantic with the total population currently estimated at 6-7 million pairs (Harris & Wanless 2011). However, over the last 20 years numbers at many colonies in Norway, Faroe Islands, Iceland and northern Britain have declined substantially (Harris & Wanless 2011). Although the species has been extensively studied during the breeding season (Lowther *et al.* 2002, Harris & Wanless 2011), details of its winter ecology are little known because birds disperse widely throughout the North Atlantic and western Mediterranean (Anker-Nilssen & Aarvak 2009, Guilford *et al.* 2011, Harris *et al.* 2010, 2013, Jessopp *et al.* 2013). Most mortality of Puffins is thought to occur during the winter, so food availability may be critically important at this time of year (Harris & Wanless 2011). During the breeding season, Puffins feed their chicks, and probably themselves, almost entirely on fish 5–15 cm long but comparatively little is known of the winter diet (Harris & Wanless 2011). Anatomical features, in particular the structure of the Puffin’s tongue, which is intermediate between the large, slender, rigid tongue of the Common Guillemot *Uria aalge* which allows leverage for holding a single large prey item and the fleshy tongue of a plankton eater such as the Little Auk *Alle alle* which has to manipulate small planktonic organisms, suggest that Puffins may also eat substantial quantities of smaller prey (Bédard 1969).

The limited data on winter diet of apparently healthy, i.e. not storm driven, Puffins support this suggestion and indicate that the majority of prey are small and in some regions (e.g. Faroe Islands, Newfoundland) invertebrates as well as fish are taken (Falk *et al.* 1992, Anker-Nilssen *et al.* 2003, Hedd *et al.* 2010), although Puffins breeding in the Gulf of Maine appear to mainly feed on fish outside the breeding season (Breton & Diamond 2014, A.L. Bond unpubl. data). A major reason for the paucity of data on winter diet is the difficulty of obtaining food samples of birds at this time. Puffins are common around the Faroe Islands during the winter and ringing recoveries and results from geolocators over the winter show that most of these birds come from Norwegian and Scottish populations rather than from Faroese colonies (Harris *et al.* 2013, Hammer *et al.* 2014). Puffins are legally shot at sea for human consumption in the Faroe Islands between 1 October and 20 January, providing us with the opportunity to collect stomach contents from a relatively large number of birds. Our main aim was to describe the diet of Puffins using this wintering area with respect to both the frequency of occurrence of prey types and their contribution in terms of biomass. Opportunistically collected data, as was the case here, are not ideal for investigating differences in diet associated with date, sex or age as they are typically unbalanced. However, within the limits imposed by the sampling protocol, our second aim was to examine whether such effects were apparent in Puffin diet.

METHODS

Puffins were legally shot by hunters on an opportunistic basis at sea off the Faroe Islands during the winters of 2008–09, 2009–10 and 2010–11 (Table 1, Fig. 1). Birds were aged using bill characteristics and classified as first-year or older (Harris 2014). Fifty-three older birds were sexed by examination of the gonads. Stomachs collected at the same date and place are termed batches.

The stomach (proventriculus and gizzard) was removed, usually within 24 h of the bird being shot, cut open and preserved in 70% alcohol. In the laboratory, the contents were spread out on a glass dish and any intact or reasonably intact items removed. These were assumed to have been ingested during the final feeding bout. The stomach was everted, rinsed in water and otoliths, large bones and skulls of fish, jaws of nereid polychaete worms and beaks of squid were picked out from the washings using a 3-20X binocular microscope. Some contents were little more than a soup of fragments of euphausid and/or amphipod crustacea and in these cases the numbers of tails and pairs of eyes, respectively were counted. Any remaining flesh and soft parts were digested in a warmed saturated solution of biological washing powder until only hard material remained. Items were identified to the lowest possible taxonomic level using standard guides (Sars 1895–1928, Breiby 1985, Härkönen 1986, Watt *et al.* 1997, Leopold *et al.* 2001, pers. reference material) and the assistance of acknowledged experts in specific groups (polychaetes: P. Olive and P. Gardwood, crustacea: J. Fraser and J. Clarke). Sandeels Ammodytidae were assumed to be Lesser Sandeel *Ammodytes marinus* (hereafter sandeel) since this is by far the commonest species in the area (Eliasen *et al.* 2011). The otoliths of some very small fish could not be assigned to a species and were termed ‘fry’.

After identification, all but the smallest otoliths were paired and the number of individual fish calculated from numbers of pairs and remaining singles. Upper and lower squid beaks and left and right nereid jaws were treated in a similar manner. All prey remains were photographed with a Zeiss camera stereoscope (Stereo Discovery V8 Achromat S, 0.63 x FWD 115 mm) and maximum length and breadth were measured using Axiovision software (AxioVs 40 v.4.8). Each otolith was assigned to one of five classes to allow for the effects of the digestive acids: pristine, slight wear, moderate wear, severe wear and too worn to allow the calculation of length for fish size estimation. For all but the last class, otolith lengths were corrected for digestion using species-specific correction factors based on comparisons with the median sizes of otoliths in each wear class (Leopold *et al.* 1998, 2001) and the total lengths and masses of the fish from which they originated were calculated using published relationships and unpublished data (Breiby 1985, Härkönen 1986, Sameoto 1988, Leopold *et al.* 2001). In stomachs with unidentifiable minute otoliths from fry or with large numbers of very small, similarly sized otoliths (e.g. of Silver Rockling *Gaidropsarus argentatus* (hereafter rockling, since not all could be identified to species)), otoliths were sorted into batches of similar size, counted and the number of fish present taken as half the total. In such cases, the largest and smallest otoliths in each batch were measured and sizes of the other otoliths in that batch were estimated by intrapolation and the masses calculated. The length frequency distribution of sandeels (later) suggested that several age classes were involved. The smallest individuals (≤ 6.7 cm) lacked growth rings in the otoliths and were assumed to be 0 group (hatched during the previous 12 months). Individuals 6.8–11.9 cm long were classed as 1 group (second year of life), those 12.0–16.0 cm long as 2 group (third year of life) and those > 16 cm as older. Pearlsides *Maurolicus muelleri* < 2.5 cm were classed as small, those 2.5–5.3 cm as medium and those > 5.3 cm as large. Intact crustacea were measured from the end of the rostrum to the tip of the telson. For jaws of nereids, a series of 11 measured pristine ’reference‘ jaws corresponding to worms in 1-cm length classes based on published jaw length to worm length relationships (Olive & Garwood 1981) spanning the size range were lined up. Jaws from each stomach were sorted accordingly (Fig. 2) and the number of worms in each size class was taken as the number of pairs and singles, or as the maximum count of right or left jaws where there were very large numbers. Lengths and masses of nereids were calculated using the relationships: Length (cm) = 2.25 * jaw length (mm) - 0.88 and Log mass (mg) = 3.4 * log jaw length (mm) + 1.03, respectively (after Olive & Garwood 1981). Masses of crustacea were calculated using relationships in Ridoux (1994) except for *Hyperia galba* where mass (mg) = 0.007 * length (mm)$^{3.6718}$ (A. Hedd unpubl. data).

For dietery analysis, prey species and/or size categories were grouped as follows: 0 group sandeel, large sandeel, mesopelagic fish, rockling, large fish (species other than sandeel where some recorded individuals were longer than 7 cm), fry (other fish species which did not reach 7 cm), nereid worm, crustacea and squid (see Table 2 for details of groupings). Diet was expressed in terms of (1) frequency of occurrence of prey types in stomachs and (2) percentage of biomass of each prey type inferred from prey hard parts (otoliths, nereid jaws, squid beaks and more or less intact crustacea) totalled within a month or winter. Biomass data were converted to energy values using published relationships (Pedersen & Hislop 2001 for fish, Thayer *et al.* 1973 for invertebrates). To allow for the skewed distribution of the data, lengths and masses of prey are presented as geometric means with 95% confidence limits. In an attempt to reduce bias due to overestimation of species that are more resistant to digestion, the occurrence of recently ingested prey (found in 175 of 176 stomachs) as indicated by undigested flesh, parts of vertebral columns or pristine otoliths was used to describe what birds had eaten just prior to being shot.

The similarity between stomach contents was calculated using the Jaccard Similarity Measure (Jaccard 1900) and the presence/absence of recent prey groups. Seasonal, sex and age class differences in diet were tested using Permanova (Anderson 2001, McArdle & Anderson 2001). All statistical analyses were performed using Primer 6 (version 6.1.16, Clarke & Gorley 2006). *P*-values are determined by comparing the test statistic to a null distribution generated by permutation. We choose 4999 permutations and if fewer unique permutations were possible we report the number of permutations ($N_{\mathrm{perm})}$ used.

RESULTS

Prey species

Fish

The remains of 3308 fish comprising 20 species were identified and measured (Table 2). However, three species accounted for 87.7% of the total number of prey items: sandeels (46.4%), rocklings (22.5%) and Pearlsides (18.8%). The individual fish were mostly small, with a median length of 4.3 cm and mass of 0.25 g, with only 5% being longer than 10 cm and 0.4 % heavier than 10 g (Fig. 3).

Crustacea

The remains of 1267 crustacea were recorded: Amphipods were the most numerous (789 *Hyperia galba,* 70 *Themisto gaudichaudi,* 2 *T. abyssorum*). Euphausids (404) were also common but the majority were damaged, making specific identifications difficult. However, most appeared to be *Thysanoessa inermis* with a small number of another species (possibly *Nematoscelis megalops*). One decapod larva (possibly Shore Crab *Carcinus maenas*) and one isopod (*Idotea neglecta*) were also recorded. All crustacea were very small with lengths ranging 0.7–2.4 cm (Table 2).

Polychaetes

The jaws of 2328 nereids were found but only five stomachs contained parts of undigested worms. Four of these stomachs came from a single day and contained the fresh remains of several hundred sexually immature (i.e. not epitokous) *Nereis pelagica,* a species common over the Faroe shelf. However, the bulk of the material consisted of jaws that could not be assigned to a species so could have included *N. zonata*, a less common species in the area (Kirkegaard, 1998).

Chaetognatha

A single unidentifiable individual that was found was included with the crustacea for analyses.

Frequency of occurrence of prey types in Puffin diet

The most frequently recorded prey remains overall were 0 group sandeels, which were found in 82% of stomachs (Table 3). The next most frequent groups were mesopelagic fish (52%) and nereids (41%). Rockling occurred in 36% of stomachs, crustacea in 35% and large sandeel and other large fish were both recorded in 32% of stomachs. In terms of frequency of occurrence of fish or invertebrate prey in the diet, the former were markedly more important, being present in 98% of stomachs compared to only 43% with invertebrates. Considering only undigested items that were assumed to reflect what birds had been eating immediately prior to being shot, indicated that 77% contained sandeels, 47% contained mesopelagic fish, 36% contained rockling/fry, 35% contained crustacea, 7% contained other large fish, and 3% contained nereids (Table 4).These frequencies were significantly different from those for the total material ($\chi^2 = 54.4$, df = 5, $P < 0.001$ after pooling the two age groups of sandeel and ignoring the single squid beak). This difference was due mainly to the higher frequency of nereid jaws in the overall diet ($\chi^2 = 4.8$, df = 4, $P = 0.31$ after removing nereid jaws).

Biomass of prey in Puffin diet

Nereids (41%), large sandeel (23%) and large fish (17%) made up the bulk of the diet in terms of biomass. Due to their very small masses (< 0.5 g), 0 group sandeel, mesopelagic fish, fry, rockling and crustacea together made up only 17% of the total biomass (Table 3). The relative importance of fish and invertebrate prey in the diet as indicated by biomass was

55% fish and 45% invertebrates. In terms of energy, large fish and large sandeels made up 46% of the total diet although they accounted for only 9% of total items.

Effects of date, sex and age on diet

The heavily unbalanced dataset hindered comparisons between winters, sexes and age-groups in one analysis (Table 1). Batches of birds were nested within the three winters and a number of hypotheses were tested on different subsets of the data. There were highly significant differences in stomach contents between batches (Permanova using all data with Winter as a fixed effect and Batch as a nested factor within winter; $F_{16,156} = 4.83$; $P = 0.0002$, $N_{\text{perm}} = 4966$). The different winters also had a significant effect on stomach composition ($F_{2,28} = 4.57$, $P = 0.0024$, $N_{\text{perm}} = 4987$). Variation between stomachs within batches or within winters varied much less (approximately 50%) than between batches and winters. In the batch from December 2010, three of the four individuals had a very different diet compared to all other birds, consisting solely of nereid worms. When this batch was excluded from the analysis, the *P*-values remained the same, but the variation within batches was only 37% of the variation between individual birds.

The proportions of first-winter birds in the samples varied over the winters with the proportion in the 2009/10 winter (45/96 = 0.46) being significantly higher ($\chi^2_2 = 33.9$, $P < 0.001$) than those in 2008/9 (4/23 = 0.18) and 2010/11 (2/57 = 0.04). The actual difference could well have been even more marked early in that winter since 43 of the 51 adults in the 2009-10 winter were sampled after 28 December, a period not covered in the other two years. The predominance of young birds in the early part of this particular winter appears to be real since the hunters themselves remarked on this. The reason for annual differences in the ages of Puffins around the Faroes is currently unknown.

Batches tended to be made up of either first-winter or older birds. Thus a batch effect may obscure an age effect. To test for an effect of age the data were restricted to only include batches in which both ages were present, Permanova indicated a significant interaction between batches (nested within winters) and age ($F_{6,71} = 2.067$, $P = 0.0224$, $N_{\text{perm}} = 4980$) indicating that the effect of one factor depends on the levels in the other or vice versa. This precludes the testing of the main effect of age (or batch). Only in one batch were there sufficient numbers of male (12) and female (15) Puffins to test for sex differences in diet and here there was no evidence of a sex difference ($F_{1,25} = 0.21$, $P = 0.832$, $N_{\text{perm}} = 43$).

DISCUSSION

This opportunistic study, based on birds shot legally for food, quadrupled the number of diet samples obtained for Atlantic Puffins outside the breeding season. Our data show that birds wintering around the Faroe Islands took a wide variety of fish and invertebrates. Although the majority of items were small (< 5 cm in length), large fish, large sandeel and nereid worms were most important in biomass terms and dominated energetically. Puffin diet appeared to be governed by fine-scale spatio-temporal processes resulting in relatively similar diets of birds sampled concurrently in space and time. Within-batch variation in diet was therefore generally markedly less than variation between batches. Stomachs from the same batch were often dominated by a particular prey type e.g. small sandeel, pearlsides or nereid worms, indicating that during winter Puffins are generalists rather than specialists, switching between different prey types and probably taking anything suitable that they encounter.

Falk *et al.* (1992) obtained Puffins shot in this area in January-March 1987 and 1988. Like us, they found that birds had eaten a variety of fish and invertebrates but their results differed slightly in a number of respects. First, they did not record any Pearlsides, which were present in 52% of our stomachs. Second, they reported Capelin *Mallotus villosus* in 24% of stomachs, whereas we did not record this species. Capelin are at the southern edge of their range around the Faroe Islands (Muus *et al.* 1999), so perhaps were not present in the area during the times that our birds were shot. Third, there were differences in the frequency of all the main prey categories between the two time periods. However, the small number of stomachs in 1987-88 (*n* = 21) makes it risky to conclude that the differences reflect a real change in diet.

All the Puffins sampled at the Faroe Islands were collected in relatively shallow waters over the shelf (< 130 m). In contrast, 14 Puffins drowned on long lines set in the Norwegian Sea well beyond the 2000 m isobath had a rather different diet, having fed mainly on Glacier Lanternfish *Benthosema glaciale* and the squid *Gonatus fabricii* with few crustacea and nereids (Falk *et al.* 1992). The other data from the East Atlantic refer to birds collected in the late summer or spring. Five birds shot off east Scotland in August contained the remains of clupeids, probably very small Herring *Clupea harengus* (four birds), Gadidae (two birds) and sandeels (one bird) (Tasker *et al.* 1986) whereas Puffins sampled at sea off Røst, Norway on 12 April 1996 had eaten many nereid worms (Anker-Nilssen *et al.* 2003). In the West Atlantic, 10 first-winter Puffins shot off Newfoundland in October had eaten both fish (six stomachs) and crustacea (eight stomachs) and, although there were more crustacea than fish, the latter dominated the biomass due to the Capelin eaten being 13–14 cm long (Hedd *et al.* 2010).

The only other information on winter diet known to us comes from Puffins found dead on beaches. Of 89 stomachs with any remains from north and north-east Scotland, 72% contained otoliths and bone fragments of fish including gadoids, sandeel, Sprat *Sprattus sprattus*, goby sp., Three-spined Stickleback *Gasterosteus aculeatus* and Fifteen-spined Stickleback *Spinachia spinachia*, Hooknose *Agonus cataphractus* and Snake Pipefish *Entelurus aequoreus* (Harris & Wanless 2011, unpubl. data). All the pipefish records (12) were in the 2005/06 winter which coincided with a population explosion of this species

(Harris *et al.* 2007). Nereid jaws were present in 28 (35%) stomachs and one stomach contained a squid beak. No crustacea were recorded. Four birds from the Netherlands had remains of Three-spined Sticklebacks and another contained small sandeels whereas three stomachs from the Azores had squid and another had unidentified fish (Kees Camphuysen unpubl. data). While these results need to be viewed with caution, because Puffins found dead on beaches probably died of starvation and may thus have eaten species not normally taken, they further emphasise that outside the breeding season Puffins take a wide variety of prey.

Scaling up frequency data from stomach contents to express diet in terms of biomass and energy contribution involves a number of assumptions and caveats, notably about differential digestion of prey. Puffins completely digest a fish within 5–6 h of its ingestion (Hilton *et al.* 1998) and stomachs from birds killed by humans or other predators at the colony are usually empty (pers. data). However, larger items e.g. bones and otoliths of large fish and harder items e.g. beaks of squid and the jaws of nereids will probably persist and remain recognizable for days whereas the bones and otoliths of small fish and small crustacea may be completely digested within hours (Wilson *et al.* 1985, Jackson & Ryan 1986, Tollit *et al.* 1997, but see Browne *et al.* 2002 and Arim & Naya 2003 who warn that the relative contribution of large, but rare, prey may also be underestimated by using otoliths). Thus while we found good agreement between recently ingested prey and overall diet in terms of the frequency of occurrence of small fish and crustacea (Tables 3a & 4), large fish, nereids and squid were more common in overall diet in accord with their expected longer persistence. More generally, the importance of nereids could be overestimated since the jaws of these species are made of protein tanned with heavy metals including large amounts of zinc and some copper (Lichtenegger *et al.* 2002), which makes them much more resistant to acid digestion compared to the remains of fish and crustacea. However, four stomachs from a single day in December 2010 contained virtually nothing except nereids. Measurements of the jaws suggested a biomass of 980 g equivalent to > 20% of the total calculated biomass for the entire study implying that these worms must periodically be a major component of the diet of Puffins in this area. Furthermore, a DNA-based study using faecal material collected from breeding Puffins in Canada found an even higher frequency of nereids (60–80%) compared to the frequency in our winter stomachs (41%) (Bowser *et al*. 2013). Ideally, captive studies are needed to quantify these biases and improve the accuracy of the biomass estimates. However, until these are carried out, the potential for certain prey types to be over-represented needs to be recognized, particularly if the results are being used in predator consumption or food web models.

Information on winter diet also provides insights into Puffin feeding behaviour at this time. Puffins catch their prey by diving from the surface. Data collected using time-depth recorders on Puffins from the Isle of May, whose winter range includes the Faroe Islands, showed that the median maximum dive depth of 24 000 dives made by four Puffins between August and December was 4.5 m, with the deepest dive being 39 m (Harris & Wanless 2011). The median water depth read off navigation charts where our stomach samples were collected was 77 m (n = 176, range 56–151 m) so it is unlikely that the shot Puffins had been feeding on or near the sea floor. All the fish and crustaceans recorded in the diet could potentially have been caught near the surface or in mid-water. However, *Nereis pelagica*, the only nereid identified, spends most its life on the sea floor and only the mature epitokous or spawning form is thought to regularly leave the seabed. Intriguingly, all the worms that were intact enough to examine critically appeared to be the atokous or sexually immature stage that would have been expected to have been in the benthos. Nereids are regularly recorded in the diet of other seabirds. For instance, Northern Fulmars *Fulmarus glacialis* consumed large numbers at Bear Island and other northern colonies and *N. pelagica* occurred in 16% of birds shot in Greenland (Phillips *et al.* 1999). Nereids were also recorded in 52% and 13% of the stomachs of young and full grown Northern Fulmars in and around the Faroe Islands with the incidence being highest during July-September suggesting summer spawning of these worms (Danielsen *et al.* 2010). Similarly, the most common item recorded in the stomach contents of Black-legged Kittiwakes *Rissa tridactyla* breeding on Helgoland was nereids (Markones *et al.* 2009). Nereids have also been recorded in the diet of Common Guillemot *Uria aalge*, Razorbill *Alca torda,* Great Cormorant *Phalacrocorax carbo* and European Shag *Phalacrocorax aristotelis* (Blake *et al.* 1985, Barrett *et al.* 1990, Leopold & van Damme 2003). As far as we know, the winter records of nereids in the diets of seabirds that feed at or near the sea surface refer to jaws found in stomachs or to birds seen feeding directly on swimming epitokes. Although the atokous forms are quite capable swimmers, and in some circumstances may leave their burrows and swim freely (P. Olive pers. comm.), they would not have been expected near the surface in deep water far from land. Obviously, more research is needed into the interactions between seabirds and polychaete worms.

Several authors have suggested a possible link between winter movements of Puffins and/or variation in overwinter survival to spatial or temporal changes in prey availability. For example, Jessopp *et al.* (2013) documented that after breeding some Irish Puffins migrated rapidly to waters off Newfoundland. They speculated that this was to exploit the seasonally high abundance of Capelin and sandeels occurring in that area before moving back into the central northeast Atlantic to feed predominantly on zooplankton for the remaining winter period. Breton and Diamond (2014) found that more than half of the variation in annual survival of adult Puffins breeding in the Gulf of Maine was explained by fishery landings of Herring (52%) and of 1 group Herring in the diet of Puffin chicks (51%). However, as noted by the authors, key data on the diet of these adults during the winter when most mortality occurs are currently lacking. Thus, while there is strong correlative evidence the causal link cannot be tested.

In conclusion, although during the breeding season Puffins appear to be mainly piscivorous, in the winter they have a much broader diet that includes substantial numbers of small invertebrates. Even so, much of the energy that they obtain appears to come from fish 6–15 cm long. Presumably a Puffin will take whichever species, fish or invertebrate, are available at any time and place. Although we know of no quantitative data, it seems highly likely that within the depth range of a foraging Puffin, planktonic crustacea and very small fish will be more numerous than large fish. A Puffin's diving strategy is to make large numbers of relatively short and shallow dives (Harris & Wanless 2011). For instance, the average number of dives per day made by two Puffins fitted with time-at-depth recorders in October was 965 (range 622–1257) with diving activity accounting for about 60% of the hours of daylight (unpubl. data). This suggests that Puffins spend much time catching small but numerous prey while waiting for the occasional large fish or swarm of nereid worms near the surface. Dietary information from more areas and data on the numbers and distribution of a wide variety of small fish and invertebrates are needed to test whether this is a deliberate strategy.

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Table 1. Details of Atlantic Puffins shot in the Faroe Islands that contained food remains. The locations where birds were collected are shown in Figure 1.

Batch No.	Winter	Date	Number of stomachs	First-year	Adult	Male	Female
1	2008-09	18 November	1	0	1	0	1
2	2008-09	22 December	20	3	17	0	0
3	2008-09	27 December	2	1	1	0	0
4	2009-10	1 October	17	15	2	0	0
5	2009-10	5 October	6	5	1	2	4
6	2009-10	16 October	8	8	0	3	5
7	2009-10	19 October	3	1	2	3	0
8	2009-10	24 October	5	5	0	0	0
9	2009-10	21November	6	6	0	0	0
10	2009-10	24 November	5	3	2	0	0
11	2009-10	3 December	3	2	1	0	0
12	2009-10	29 December	6	0	6	0	0
13	2009-10	1 January	5	0	5	0	0
14	2009-10	28 January	32	0	32	0	0
15	2010-11	9 October	19	0	19	3	3
16	2010-11	12 October	30	1	29	12	15
17	2010-11	25 October	3	1	2	0	0
18	2010-11	30 October	1	0	1	2	0
19	2010-11	7 December	4	0	4	0	0
Total			176	51	125	25	28

Table 2. Numbers and calculated lengths and masses of prey recorded from the stomachs of Atlantic Puffins shot during the winter around the Faroe Islands. The groupings in bold are those used for the analyses of diet (see text).

				Length (cm)		Mass (g)	
		Total items (*n*)	Lengths estimated (*n*)	Geometric mean (cm)	95% CI	Geometric mean (g)	95% CI
Sandeel – 0 group							
Ammodytes marinus 0 group	Lesser Sandeel	1071	710	4.8	4.7–4.9	0.2	0.19–0.21
Sandeel – large							
Ammodytes marinus 1 group	Lesser Sandeel	427	419	9.1	9.0–9.2	1.8	1.71–1.83
Ammodytes marinus 2 group	Lesser Sandeel	35	32	13.6	13.3–13.9	7.1	6.63–7.70
Ammodytes marinus older	Lesser Sandeel	1	1	19.1		23.1	
Mesopelagic fish							
Maurolicus muelleri small	Pearlsides	116	78	2.4	2.3–2.5	0.05	0.04–0.06
Maurolicus muelleri medium	Pearlsides	495	241	4.0	3.9–4.1	0.4	0.35–0.45
Maurolicus muelleri large	Pearlsides	11	9	6.1	6.0–6.2	1.5	1.40–1.62
Benthosema glaciale	Glacier Lanternfish	17	13	2.4	1.7–3.3	0.2	0.06–0.57
Rockling							
Gaidropsarus argentatus	Silver Rockling	745	725	3.0	2.9–3.0	0.2	0.15–0.16
Large fish							
Trisopterus esmarkii	Norway Pout	99	94	9.1	8.8–9.5	4.7	4.22–5.33
Merlangius merlangus	Whiting	13	12	8.3	7.4–9.5	4.4	3.01–6.30
Lysenchelys sarsi	Sars' Eelpout?	9	1	4.2		0.7	
Micromesistius poutassou	Blue Whiting	8	7	7.4	4.6–11.9	2.6	0.69–10.16
Platichtys flesus	Flounder	7	6	8.0		5.2	
Unidentified fish		2	2	7.1		1.7	
Lycodes vahli	Vahl's Eelpout	2	1	8.1		2.5	

Gadidae sp	Unknown	3	1	7.6		3.1	
Gadus morhua	Atlantic Cod	1	1	13.3		20.7	
Scomber scombrus	Mackerel	1	1	17.4		45.8	
Fry							
Unidentified fry		120	110	3.8	3.6–3.9	0.1	0.07–0.10
Crystallogobius linearis	Crystal Goby	109	102	4.2	4.1–4.4	0.4	0.35–0.41
Limanda limanda	Dab	8	7	4.0		0.5	
Phycis blennoides	Forkbeard	3	3	4.1	2.2–7.7	0.4	0.05–2.78
Trisopterus luscus	Bib	1	1	1.1		0.8	
Cyclopterus lumpus	Lumpsucker	1	1	2.3		0.5	
Gasterosteus aculeatus	Three-spined Stickleback?	1	1	4.3		0.6	
Aphia minuta	Transparent Goby	1	1	3.0		0.0	
Pomatochistus pictus	Painted Goby	1	1	1.0		(0.06)	
Polychaeta							
Nereis pelagicus	Nereid worm	2328	2327	6.4	6.3–6.5	0.6	0.56–0.60
Crustacea							
Hyperia galba[3]	Amphipod	789	436	1.3	1.2–1.3	0.08	0.07–0.08
Themisto gaudichaudii[3]	Amphipod	70	29	1.0	0.8–1.1	0.02	0.02–0.03
Themisto abyssorum	Amphipod	2	2	1.0	0.8–1.1	0.02	0.02–0.04
Thysanoessa inermis[3]	Euphausid	404	6	1.8	1.3–2.5	0.06	0.06–0.06
Idotea neglecta	Isopod	1	1	3.0		0.10	
Carcinus maenas larva	Common Shore Crab	1	1	0.5		(0.01)	
Chaetognatha							
Chaetognatha sp.	Arrow worm	1	0	1.0		(0.01)	
Squid							
Gonatus fabricii?	Squid	15	0	?		(3.0)	

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[1] Lengths and masses calculated from measurements of otoliths (fish) or jaws (Polychaeta).

[2] Masses in brackets were assumed.

[3] Specific identifications were based on the numbers of individuals that were measured.

Table 3. Diet of Atlantic Puffins based on all remains in stomachs expressed as (a) monthly frequency of occurrence, (b) monthly proportion of calculated biomass and (c) total calculated energy value (kJ). Proportions > 0.50 are in bold except for the month with only a single stomach.

Winter	Month		0 sandeel	Large sandeel	Mesopelagic fish	Rockling	Fry	Large fish	Crustacea	Nereids	Squid
(a) Frequency		Stomachs (n)									
2008-09	November	1	1.00	0.00	1.00	0.00	1.00	1.00	1.00	1.00	1.00
2008-09	December	22	**0.73**	0.05	**0.91**	0.14	0.00	0.14	**0.64**	**1.00**	0.05
2009-10	October	39	**0.79**	0.46	0.46	0.18	0.00	0.13	0.13	0.08	0.05
2009-10	November	11	**1.00**	0.09	0.36	0.09	0.18	0.00	0.27	**0.73**	0.00
2009-10	December	9	**1.00**	0.44	**0.56**	0.11	**0.89**	0.33	0.44	**0.78**	0.00
2009-10	January	37	**0.84**	0.81	**0.57**	0.00	0.38	0.49	**0.92**	0.43	0.16
2010-11	October	53	**0.87**	0.06	0.40	**0.94**	0.00	0.49	0.00	0.21	0.02
2010-11	December	4	0.00	0.00	0.25	0.25	0.00	0.00	0.25	**1.00**	0.00
Total		176	**0.82**	0.32	**0.52**	0.36	0.14	0.32	0.35	0.41	0.06
(b) Biomass		Biomass (g)									
2008-09	November	23	0.02	0.00	0.12	0.00	0.00	0.21	0.11	0.14	0.39
2008-09	December	525	0.02	0.01	0.18	0.00	0.05	0.13	0.01	**0.64**	0.01
2009-10	October	381	0.09	**0.52**	0.21	0.01	0.00	0.09	0.00	0.07	0.02
2009-10	November	212	0.25	0.00	0.07	0.05	0.00	0.00	0.01	**0.62**	0.00
2009-10	December	216	0.14	0.08	0.04	0.00	0.22	0.31	0.04	0.39	0.00
2009-10	January	1589	0.04	**0.52**	0.04	0.00	0.22	0.27	0.05	0.03	0.02
2010-11	October	622	0.12	0.04	0.02	0.31	0.26	0.38	0.00	0.10	0.01
2010-11	December	980	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**	0.00
Total		4549	0.05	0.23	0.06	0.03	0.01	0.17	0.02	0.41	0.01
(c) Energy value		kJ									
Total		20343	0.04	0.25	0.10	0.05	0.01	0.21	0.02	0.31	0.01

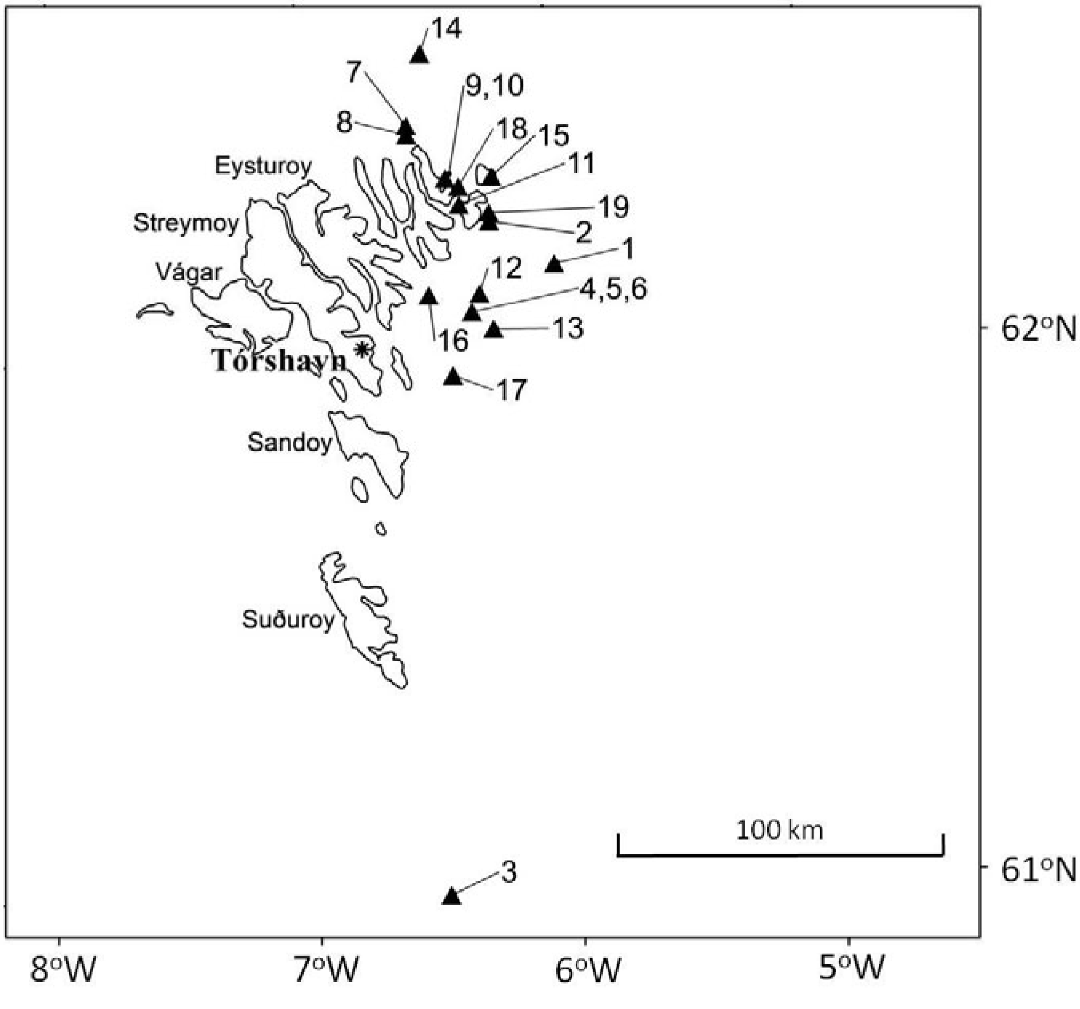
Table 4. Frequency of occurrence of prey groups in the stomachs of Atlantic Puffins based on recently eaten food (intact or undigested items). Proportions > 0.50 are in bold except for the month with only a single stomach.

Winter	Month	Stomachs (n)	Sandeel	Mesopelagic fish	Rockling/Fry	Large fish	Crustacea	Polychaetes	Squid
2008-09	November	1	0.00	1.00	0.00	0.00	1.00	0.00	0.00
2008-09	December	22	0.45	**0.82**	0.14	0.09	**0.64**	0.00	0.00
2009-10	October	38	**0.85**	**0.55**	0.18	0.03	0.13	0.00	0.00
2009-10	November	11	**1.00**	0.45	0.00	0.00	0.27	0.00	0.00
2009-10	December	9	**1.00**	**0.56**	0.22	0.00	0.44	0.00	0.00
2009-10	January	37	**0.73**	**0.54**	0.08	0.03	**0.92**	0.03	0.00
2010-11	October	53	**0.87**	0.23	**0.89**	0.17	0.00	0.00	0.00
2010-11	December	4	0.00	0.00	0.25	0.00	0.25	**1.00**	0.00
Total		175	**0.77**	0.47	0.36	0.07	0.35	0.03	0.00

Figure 1. Locations around the Faroe Islands where Atlantic Puffins were sampled between 2008 and 2011. Numbers refer to batches of stomachs listed in Table 1.

Figure 2. *Nereis pelagicus* sorting disc developed for this study. *Nereis* jaws found in Atlantic Puffin stomachs were matched to 11 sets of reference jaws (visible under the lower left of each label). In this particular sample, 0 jaws of size class 1 were found (only 2 reference jaws are shown); 8 jaws (4 pairs) of size class 2 (represented by 3 reference jaws); 25 jaws of size class 3, etc, until 6 jaws of size 9.

Figure 3. Frequency distributions of the calculated lengths of fish and nereid worms eaten by Atlantic Puffins.



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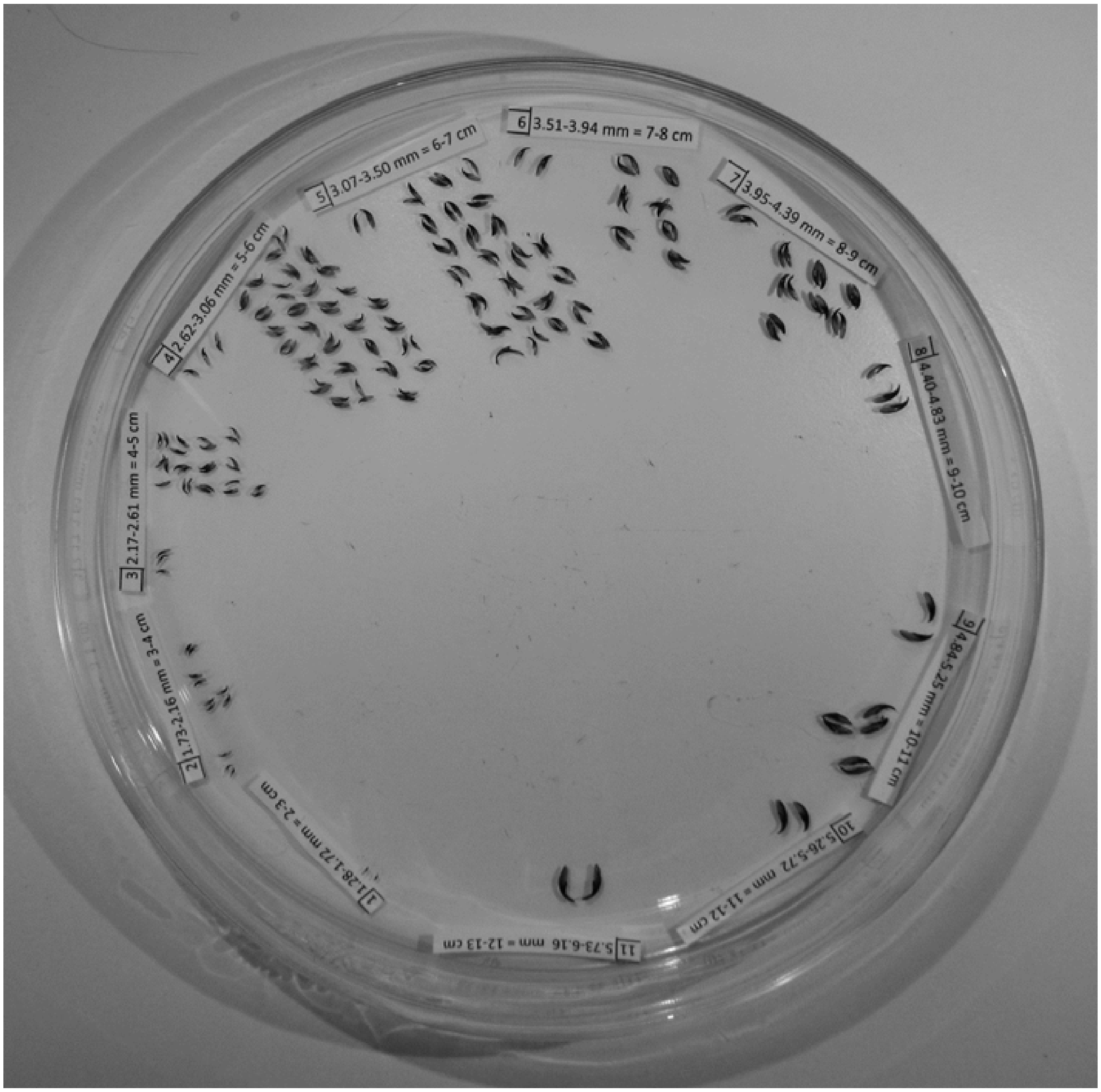

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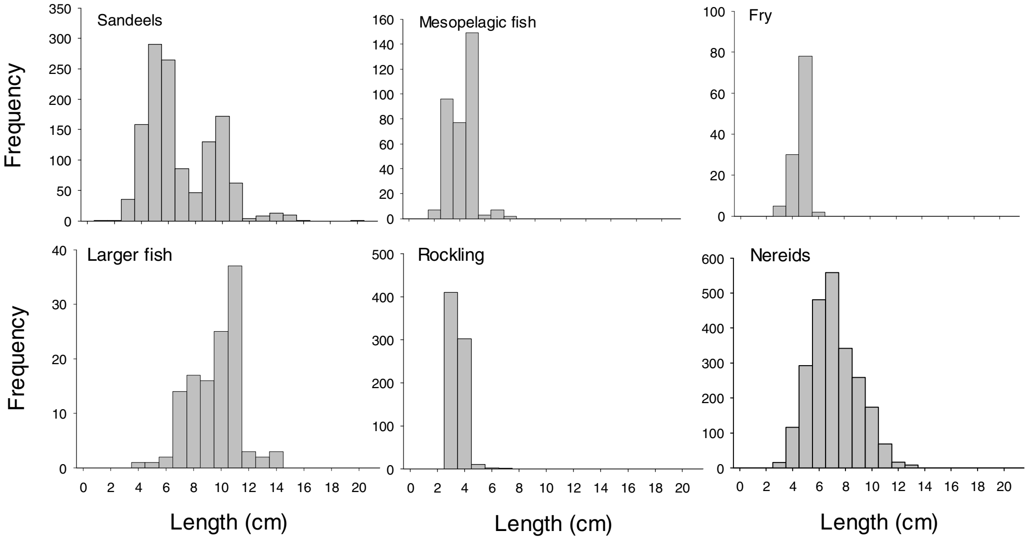

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