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An estimate of summer food consumption of six seabird species in Iceland

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The diet of the six most numerous seabird species found in Iceland was investigated during the summers of 1994 and 1995. A total of 1481 stomachs was analysed from common guillemots (*Uria aalge*), Brünnich's guillemots (*U. lomvia*), razorbills (*Alca torda*), puffins (*Fratercula arctica*), kittiwakes (*Rissa tridactyla*), and northern fulmars (*Fulmarus glacialis*). The combined summer populations of these species in Icelandic waters are estimated at eighteen million individuals. All species except the fulmar rely heavily on capelin (*Mallotus villosus*), sandeel (*Ammodytes marinus*), and euphausiids as food. The food of fulmars is different from the others, with discards and offal from fishing vessels probably comprising a substantial part of the summer diet. The estimated annual summer food consumption of the bird species investigated is 171 000 t of capelin, 184 000 t of sandeel, and 34 000 t of euphausiids. These estimates are likely to have wide confidence intervals but probably display the general picture. The results indicate that the consumption of capelin by seabirds needs to be taken into account when modelling trophic relationships involving capelin, for example, with commercially important fish species. Furthermore, capelin are fished commercially around Iceland and these seabird species may be eating about 8% of the total capelin biomass each summer. The results further emphasize the importance of sandeel and euphausiids as prey for the birds.

Key words: capelin, consumption, euphausiids, Iceland, sandeel, seabirds, summer diets.

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Introduction

Information on the feeding ecology of seabirds in Iceland is limited. As several species have summer populations larger than one million individuals, they may have a considerable impact on their marine environment. In this paper, we describe the summer diets of the six most numerous seabird species in Iceland. Based on these results, the total consumption of prey species, by the birds, during three summer months is estimated. Our approach is broadly similar to other studies analysing the impact of seabirds on their marine environments (e.g. Wiens and Scott, 1975; Furness, 1978, 1990; Furness and Cooper 1982; Brown and Nettleship, 1984; Furness and Barrett, 1985; Martin, 1989; Cairns *et al.*, 1990; Hatch and Sanger, 1992).

Materials and methods

We analysed the summer diets of common guillemots (*Uria aalge*), Brünnich's guillemots (*U. lomvia*), razorbills (*Alca torda*), puffins (*Fratercula arctica*), kittiwakes (*Rissa tridactyla*), and northern fulmars (*Fulmarus glacialis*). Adult birds were shot at sea on their feeding grounds, up to 130 km from their colonies. Data were collected around Iceland on 64 days between 30 May and 6 August in the summers of 1994 and 1995. Soon after collection, the stomachs were removed from the birds, split open, and preserved in alcohol. The prey were identified in the laboratory, usually to species. Wet mass for each food category was estimated by measuring hard parts of the prey and then converted to fresh mass using length–mass formulae. Our own data (unpublished) on length–mass relationships were used except in the case of squid (Clarke, 1986) and hyperiid amphipods (Pakhomov and Perissinotto, 1996). Hard parts of different prey species have been shown to be retained in the stomachs for different periods of time. In order to avoid over-representation of prey species with slowly digested hard parts, this analysis is based solely on fresh food items, defined as a measurable hard part with flesh attached. The average diet composition of each bird

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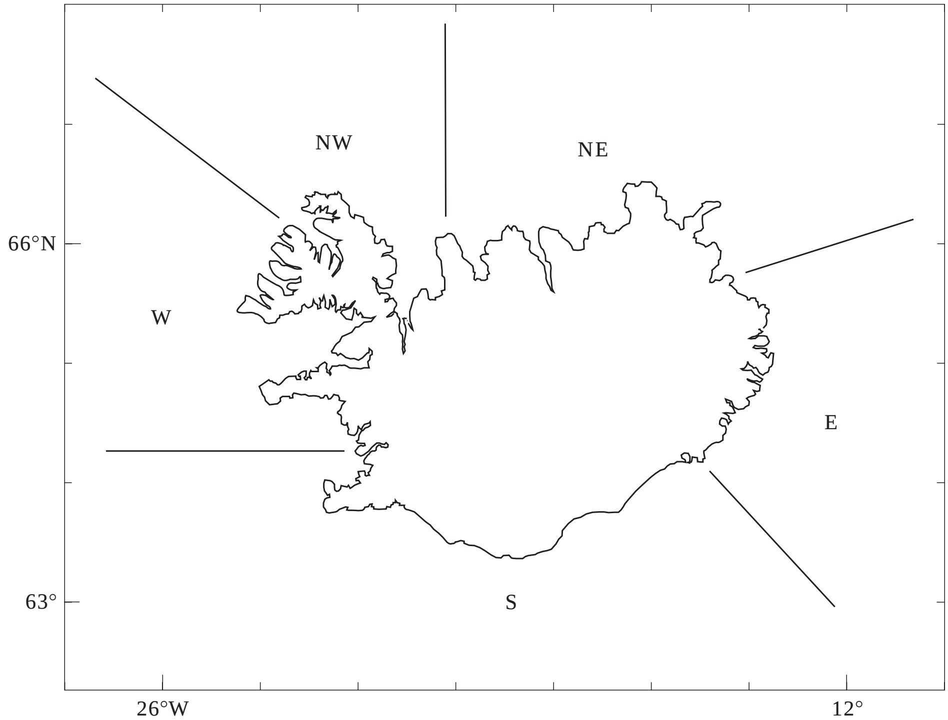

Figure 1. The division of Icelandic coastal waters into sectors based on oceanographic features and bird numbers (see text).

species was derived from the total wet mass of each food category in each area.

For the purpose of the analysis we divided the sea around Iceland into five areas (Fig. 1), based partly on differences in the distribution of breeding populations of the bird species and partly on differences in the origin of the sea water. Auks are most numerous in the west and north-west sectors, puffins are most common in the south sector, kittiwakes breed predominantly in the north-east and north-west sectors and fulmars in the

Table 1. Numbers of individuals (to the nearest thousand; % in parentheses) of six species of Icelandic seabirds during the breeding period divided between species and areas (Fig. 1). For guillemots and razorbills, the numbers are based on counts of breeding birds (Gardarsson, 1995) multiplied by 1.305 (Cairns *et al.*, 1990) to account for the non-breeders. For the other species, numbers are based on estimated numbers of breeding birds (Gardarsson, 1996, pers. comm.), in the fulmar multiplied by 1.45, in the kittiwake by 1.09, and in the puffin by 1.33 (Furness, 1978) to estimate the total populations. Key to species: CG – common guillemot, BG – Brünnich's guillemot, RA – razorbill, PU – puffin, KI – kittiwake, and FU – fulmar.

	Species					
Sector	CG	BG	RA	PU	KI	FU
East	31	6	1	931	83	218
	(1.2)	(0.4)	(0.1)	(12.7)	(6.1)	(5.0)
South	243	9	51	4522	142	1088
	(9.4)	(0.6)	(5.2)	(61.6)	(10.4)	(25.0)
West	787	313	606	1064	174	1523
	(30.4)	(20.7)	(61.3)	(14.5)	(12.8)	(35.0)
N-west	1190	1067	191	160	453	870
	(45.9)	(70.6)	(19.3)	(2.2)	(33.2)	(20.0)
N-east	339	117	139	665	511	653
	(13.1)	(7.7)	(14.1)	(9.0)	(37.5)	(15.0)
Total	2590	1512	988	7342	1363	4352

Table 2. Number of seabirds collected in this study grouped by species and sectors (Fig. 1). For species abbreviations see Table 1.

Sector	Species					
	CG	BG	RA	PU	KI	FU
East	29	6	6	30	12	26
South	40	0	30	70	35	74
West	142	42	112	95	74	81
N-west	107	72	43	47	73	66
N-east	39	3	26	37	27	37
Total	357	123	217	279	221	284
No. empty stomachs	96	22	43	100	37	120
% empty stomachs	27	18	20	36	17	42

west, north-west, and south sectors (Table 1). Polar water dominates in the north-east and east sectors, while warmer water brought by the Gulf stream is the most prominent in the south and west sectors. Sampling of the birds was based on this division into sectors (Table 2).

To calculate food consumption the number of birds must first be estimated. The number of auks is based on published estimates of their breeding populations in Iceland (Gardarsson, 1995), which is then multiplied by species-specific constants to account for the non-breeding part of the populations (Table 1). The population estimate available for the kittiwake is relatively reliable but only rough estimates on numbers of breeding birds have been made for the puffin and fulmar (Gardarsson 1996, pers. comm.). In our calculations we assume that the non-breeding birds that are present during the breeding period eat the same food and behave similarly to the breeding birds (Cairns *et al.*, 1990). Energy requirements of chicks are not considered in the present paper since they account for only a small part of energy demands of seabird populations over the breeding season (e.g. Wiens and Scott, 1975; Furness, 1978, 1990; Furness and Cooper, 1982; Brown and Nettleship, 1984; Furness and Barrett, 1985; Cairns *et al.*, 1990).

Secondly, the daily energy requirements of each species must be known. Several estimates based on different methods have been published for various seabird species. In this paper we use, where available, estimates based on the doubly-labelled water method (Lifson and McClintock 1966; Birt-Friesen *et al.*, 1989 and references therein). For razorbills, puffins, and fulmars, we use metabolic equations to estimate the energy requirements of these species (Table 3). In the case of the guillemots we use local estimates of daily energy requirements for the west and north-west sectors. For Brünnich's guillemots the estimate is 2402 kJ d^{-1} (n=9, S.D.=523) and for common guillemots it is 2034 kJ d^{-1} (n=5, S.D.=922) (Hansen and Hansen, unpublished data). In other sectors we use published estimates for the guillemots (Table 3). Based on these estimates and the diet composition in each sector the proportional energy input by each food category is calculated for each species.

Thirdly, the energy value of the different kinds of food eaten by the birds is required. We use two values for capelin (*Mallotus villosus*): for immatures 3.5 kJ g^{-1} wet mass (see Montevecchi and Piatt, 1984), and for two years and older fish 6.4 kJ g^{-1}, assuming a fat content of 10% (Vilhjalmsson, 1994) and calculated according to Montevecchi and Piatt (1984). For sandeel (*Ammodytes marinus*) we use 6.5 kJ g^{-1} (Harris and Hislop, 1978), for euphausiids 3.9 kJ g^{-1} (Lockyer, 1987), and for other food we assume a value of 5.0 kJ g^{-1} wet mass. The metabolizable energy derived from the food is then calculated assuming an assimilation efficiency of 80% (Furness, 1978).

Lastly, the time period the birds are at the breeding colonies must be defined. This may vary between species but we take a conservative approach here and use 90 days at the colonies for all species.

Table 3. The daily energy requirements of six breeding seabirds species, based on published results or estimated using metabolic equations from Birt-Friesen *et al.* (1989). For the estimates we use our own data on mean body mass of razorbills (632 g, S.D.=51, n=214), puffins (510 g, S.D.=49, n=267), and fulmars (787 g, S.D.=92, n=282). Numbers in parentheses for common and Brünnich's guillemots refer to estimates used in the west and north-west sectors (see text). For species abbreviations see Table 1.

Species	Energy required (kJ d^{-1})	Source
CG	1789 (2034)	Cairns *et al.*, 1990
BG	2080 (2402)	Brekke and Gabrielsen, 1994
RA	1245	Birt-Friesen *et al.*, 1989
PU	1065	Birt-Friesen *et al.*, 1989
KI	795	Gabrielsen *et al.*, 1987
FU	821	Birt-Friesen *et al.*, 1989

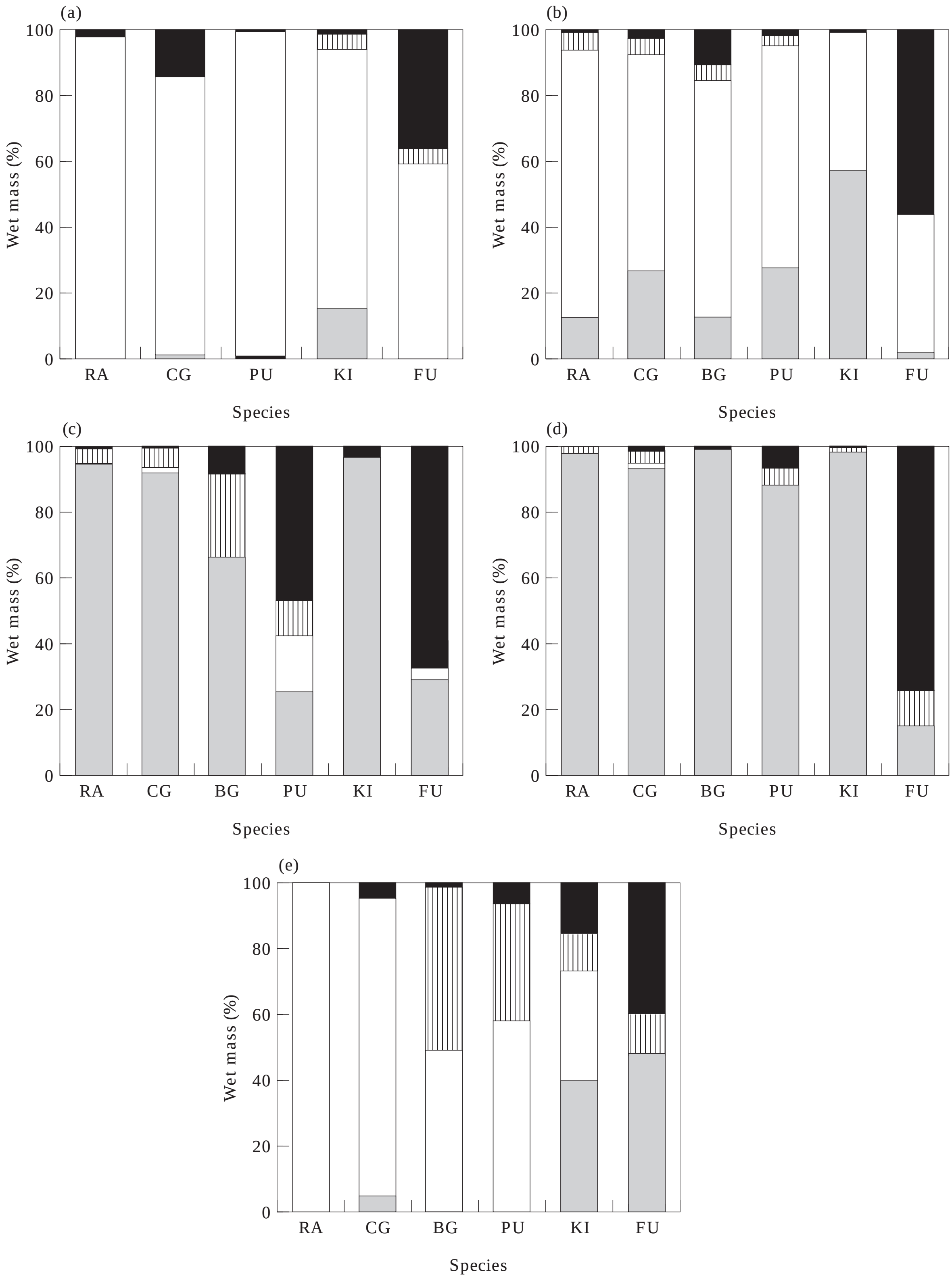

Figure 2. The summer food (in percent wet mass) of six seabird species off the coast of Iceland, (a) south sector, (b) west sector, (c) north-west sector, (d) north-east sector and (e) east sector (see Fig. 1). For species abbreviation see Table 1. ▨ Capelin; □ sandeel; ▥ euphausiids; ■ other.

Table 4. The estimated annual summer food consumption of six species of breeding seabirds in Iceland in 1994 and 1995 divided by bird species and major food items. Numbers given are in thousands of tonnes. For species abbreviations see Table 1.

Species	Capelin	Sandeel	Euphausiids	Other
RA	13.1	12.2	1.1	0.1
CG	67.8	27.9	4.6	2.4
BG	41.9	10.0	14.4	5.3
PU	23.7	109.9	9.7	4.6
KI	15.7	3.1	0.4	0.4
FU	8.5	21.3	4.0	39.6
Total	170.7	184.4	34.2	52.4

Results

Capelin and sandeel were the main summer food of seabirds in Iceland (Fig. 2a–e). In the south sector (Fig. 2a) sandeel was clearly the dominant food for all species, approaching 100% of the food of razorbills and puffins. Capelin represented 15% of the diet of kittiwakes, and in the common guillemot, 14% of the food was blue whiting (*Micromesistius poutassou*) and herring (*Clupea harengus*). Nearly 40% of the food of fulmars consisted of discards from fishing vessels, mostly blue whiting but also redfish (*Sebastes* spp.) and Norway lobster (*Nephrops norvegicus*).

In the west sector (Fig. 2b) sandeel was the most important food, with values ranging between 40 and 80%, and capelin was the main secondary food. The diet of fulmars consisted mainly of squid, amphipods, and small organic particles in addition to the 40% of sandeel.

In the north-west sector (Fig. 2c), sandeel was rarely used as food with the exception of being nearly 20% of the diet of puffins. Capelin dominated as the food of auks and kittiwakes. In addition to sandeel, the puffin diet comprised 25% capelin and 10% euphausiids, but more than 45% of the food consisted of amphipods and squid, approximately 34% and 11%, respectively. The diet of the fulmar consisted of 30% capelin and 10% euphausiids, the remainder being mainly discards from fishing vessels, with redfish, eelpout (*Lycodes* spp.), and the northern shrimp (*Pandalus borealis*) the most important (Fig. 2c).

In the north-east sector (Fig. 2d) diets were roughly similar to those of the north-west sector. Capelin was the dominant food of most species with euphausiids as secondary food. The food of fulmars was quite different from the diet of other species. The main food (75%) seemed to be discards from fishing vessels with redfish and northern shrimp of roughly equal importance. In addition to discards fulmars ate 15% capelin and 10% euphausiids.

In the east sector (Fig. 2e), sandeel again replaced capelin as the dominant fish prey. Euphausiids were important as a secondary food, notably for puffins (35%) and the few Brünnich's guillemots (50%) in the sample. Kittiwakes ate mainly sandeel and capelin but euphausiids and polar cod (*Boreogadus saida*) were also important. In the fulmar, approximately 50% of the food consisted of capelin and 10% of euphausiids, but nearly 40% was discards from fishing vessels, with roughly one-half being redfish and the other half northern shrimp.

According to calculations of the total food consumption (Table 4), we estimate that 42% of the summer food of the species studied consists of sandeel. Capelin were second in importance with 38%, but euphausiids and other food were less important with 8% and 12% respectively. Capelin was the main food of four of the species studied, the exceptions being the puffin, which relied mostly on sandeel, and the fulmar, more than one-half of whose diet was ''other'' food, mostly discards from fishing vessels.

Discussion

The results indicate the importance of pelagic fish species as food for five of the six species of seabird studied, and agree with several studies on seabird summer diets in the north-east Atlantic (see Cramp and Simmons, 1982; Cramp, 1985; Bradstreet and Brown, 1985). The importance of different prey species clearly differs between areas, which probably reflects differences in availability of the fish prey rather than demonstrating selection by the birds. Our results suggest that only fulmars are dependent on discards from fishing vessels, which is in agreement with earlier reports (see review in Cramp and Simmons, 1977).

Our results demonstrate that seabirds probably have a considerable impact on the marine environment around Iceland. Apparently, they are major consumers of their most common prey species. The birds may affect human fishing activity in two ways. Firstly, they may compete directly with the fishery for commercially important species. The only fish species exploited by Icelanders that is important to the seabirds studied is capelin. The capelin fishery concentrates on adult fish, but the birds apparently take all year classes. The relationship between summer feeding seabirds and the fishery is further complicated by the fact that only small quantities of capelin are fished during the summer and some of the capelin stock may be out of reach for breeding Icelandic seabirds (Vilhjalmsson, 1994). The consumption of approximately 171 000 t in 3 months is a substantial amount but has to be compared with the estimated biomass of the Icelandic capelin stock and the commercial catch. In the years 1991–1995, the average biomass of this stock was 2 200 000 t (S.D. = 357 000 t, n = 5) as estimated on 1 August, with the annual catch being 794 000 t (S.D. 297 000 t, n = 5) (Vilhjalmsson, 1994; Anon., 1996). The estimate of capelin stock size is thus dated late in the breeding season. Nevertheless, the six seabird species studied may consume about 8% of the total capelin stock each summer. The birds might also affect the population size of adult capelin by eating juveniles. In order to address these questions, the size and age of the capelin prey must be incorporated into models of the possible effects of seabirds on the population dynamics of capelin.

Secondly, the birds may have an effect on fisheries by competing for food with commercially important fish species, thereby reducing the fish stocks utilized by humans. Sandeel, capelin, and euphausiids are the main food of quite a number of commercial fish species. The relationship between seabirds and other species taking the same prey is, however, much too complex to be addressed here. Our conclusion is that the impact of seabirds on the marine ecosystem should be considered in all multi-species models for Icelandic waters.

We wish to conclude on a cautionary note. Sources of error in these kinds of calculations are many and can have a substantial effect on the results. All data regarding the birds and their diets are estimates and data on the numbers of puffins and fulmars can be improved. Furthermore, additional data on the distribution of the non-breeding component of Icelandic seabird populations are required. Local data on energy requirements for each species are clearly preferable to data collected elsewhere. Our own data on summer diets need to be extended, because the composition may differ between years. The results are sensitive to the amount of energy found in different food and the values we have used may have to be replaced with values obtained more locally. Nevertheless it seems likely that seabirds around Iceland consume hundreds of thousands of tonnes of capelin and sandeel each summer, and their role in trophic relationships needs to be studied further.

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