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Summer feeding strategy of the little auk (*Alle alle*) from Bjørnøya, Barents Sea

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Abstract Summer food of the little auks nesting on Bjornoya consisted of large copepods, decapod larvae and pelagic amphipods. Food items of 4–6 mm constituted the most common prey size fraction. This prey size range appears to be optimal (most profitable) with regard to the balance between mean individual mass and density of items in the surface layers of the sea. Little auks from Bjørnøya only sporadically take the abundant copepod *Calanus finmarchicus* (2–3.5 mm in length) but select the much less abundant and larger *Calanus glacialis* (3–6 mm).

Introduction

The little auk (*Alle alle*) is one of the major plankton consumers among seabirds in the northern Atlantic, from Bjornoya (74°N) in the south to Franz Josef Land (82°N) at the northern limit of its breeding distribution (Isaksen and Bakken 1995). The feeding ecology of European little auks has been studied on Spitsbergen (Norderhaug 1970; Stempniewicz 1980; Mehlum and Gabrielsen 1993) and on Franz Josef Land (Węsławski et al. 1995), but the southernmost European (except for remnant colony on Iceland-Grimsey) population of the little auk breeding on Bjørnøya has not been studied in this respect. Little auks at Bjørnøya have an opportunity to feed on different plankton communities, since at least three different types of water masses occur in the area. Bjørnøya is located at the southwestern end of the shallow Svalbardbanken. The water mass on Svalbardbanken is well mixed throughout the water column during summer and is a mixture of cold Arctic Water with melt-water from the Barents Sea ice pack. The physical oceanographic conditions in the vicinity of Bjørnøya are characterised by non-stratified Svalbardbank water close to the island, which is surrounded to the south and west by a frontal region, where Svalbardbank water mixes with warm Atlantic water. The Atlantic water contains North Atlantic Current plankton, with admixture of Norwegian Coastal Current plankton. The surface expression of the front is located near the 100-m isobath (Lee 1952; Pfirman et al. 1994; Kwaśniewski 1995; Mehlum et al. 1996). Each of these waters is characterised by distinct plankton communities (Kwaśniewski 1995), so providing different feeding conditions for little auks. Furthermore, the Barents Sea and European Arctic waters in general are regarded as very unstable systems, with pronounced year-to-year changes in the primary productivity and fish abundance (Sakshaug et al. 1994). The aim of this paper is to present data on the diet of the little auks from Bjørnøya, and their foraging strategy, and to determine to what extent the zooplankton communities' structure influences the diet and feeding grounds selection of little auk.

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Materials and methods

Quantitative plankton samples were collected with the use of a WP-2 net, of 60 cm diameter and 200 μm mesh size. Twenty-one samples from the upper water stratum (0–30 m) were considered in this study. Samples were diluted to a standard volume of 250 cm^3, preserved in 4% formaldehyde, and were finally processed half a year later in the laboratory in Poland. Five subsamples of 20 cm^3 were analysed for mesozooplankton (organisms less than 5 mm in length), while macroplankton was determined in the whole sample volume. Quantitative plankton data presented in this study were collected from r/v "Oceania" in July 1987, 1988, 1989 and 1994 in the area of Bjørnøya (Fig. 1). Additionally, six qualitative samples were collected using BONGO net (2 × 60 cm in diameter, 250-mm mesh size) vertical hauls from 50 to 0 m in July 1995. These samples were frozen onboard, weighed (wet and dry mass), analysed for energy content and later sorted into size categories. The energy content analysis was done by microbomb calorimetry at the Univeristy of Gdansk. The survey for mapping the distribution and abundance of little auks was conducted during the period 12–31 July 1993 onboard the r/v "Lance". The study area was ice free during the investigation and the vessel's speed was ca. 10 knots. The survey was performed using standardised strip transect methods (Tasker et al. 1984). A 300-m standard transect width was applied; however, during foggy conditions the transect width was reduced to 200 or 100 m. All birds observed within the transect were recorded by species, as was information on behaviour (birds flying and birds sitting on the water), age, and environmental conditions. In this paper only little auks sitting on the water are considered. Three teams alternated on 4-h watches, each watch comprising two people: one observer and one computer data-entry operator. Densities of swimming little auks were calculated using the computer programme MAPPER (Mehlum 1989) and were presented on a map as birds per km^2 in 0.25° longitude by 0.05° latitude blocks (or ca. 7.4 × 5.5 km) using the programme CAMRIS (Ecological Consulting).

Forty-seven adult little auk food samples (from different individuals) were collected between 8 and 20 July 1994 on the southern tip of Bjørnøya (colony on Alfredfjellet, facing Ellasjoen). Birds were feeding their chicks at that time. The birds were caught in the colony using the mist nets. The food was gently removed from the gular pouches with a small plastic spoon. Food samples were preserved in 4% buffered formaldehyde and analysed 4 months later in the laboratory in Poland. Each food sample was washed gently on a 0.2-mm screen, and the prey items were identified, counted, and measured (to 0.1 mm accuracy). Length of plankters was measured from the tip of the head to the end of the telson (furca in case of copepods, fins in fishes and arrow worms) excluding antennae, setae or spines. Wet weight was obtained from the formalin-preserved materials, after blotting the animal on filter paper. Dry weight was measured after 24 h of drying at 60°C. Weight measurements were performed with 0.2 mg of accuracy. In the case of small animals with a biomass below 1 mg, 10 or 20 specimens were weighed together.

Results

Zooplankton

All pelagic species identified in the little auk food were also found in the zooplankton samples (Table 1). The most common were juvenile stages of *Calanus* spp., followed by adult *Calanus finmarchicus* and smaller copepod species (*Pseudocalanus* spp., *Oithona similis*). Table 2 presents a "blind" selection of the plankton size groups regardless of their taxonomic position, obtained from BONGO net samples. It shows the highest individual caloric values among 2- to 3-mm-long plankters (mainly younger copepods) and a sharp increase of the individual plankter's weight with increasing size class. The density of particular zooplankton size categories decreased with increasing weight-and size. The most abundant were 2- to 3-mm items, and those over 4 mm were 10 times less abundant (Fig. 3). The frequency of occurrence of the particular size classes shows a different pattern. The most frequent were medium-sized organisms (3–5 mm), and those above 5 mm were much less common (Table 1).

Fig. 1 Distribution of little auks on the sea in the vicinity of Bjørnøya, July 1993. *Numbers* are given per km^2. Zooplankton sampling localities indicated with *unfilled circles*

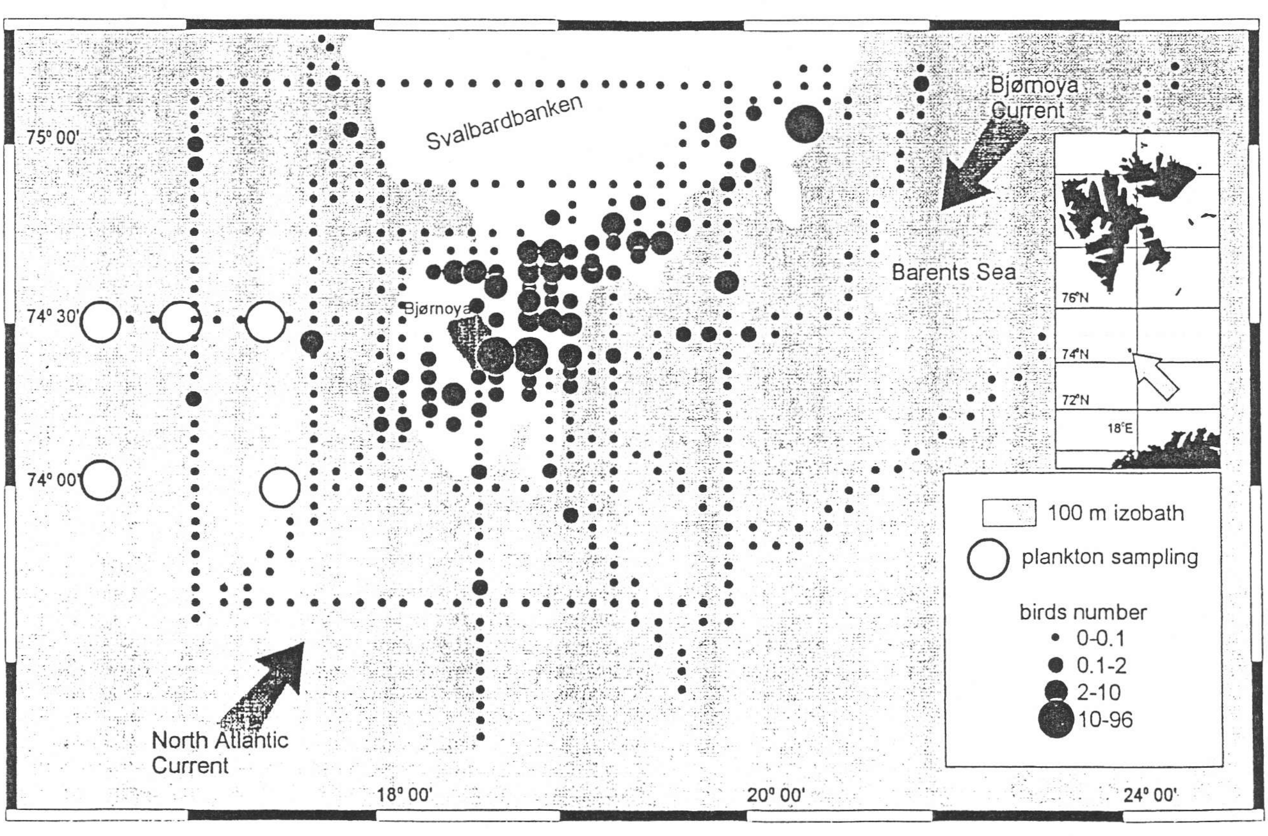

Table 1 Food content of the little auks from Bjørnøya, July 1994 and the composition of zooplankton west from Bjørnøya (*Alle alle* food $n = 47$; plankton samples $n = 21$)

Taxon	Size class (mm)	Wet weight (mg)	Bird frequency of occ. (F%)	Net frequency of occ. (F%)	Bird numerical dom. (D%)	Net numerical dom. (D%)	Net density mean (ind/m³)	Bird occur. (ind/sam.)	Bird weight dominance (%)
Acartia longiremis	1.5		0	14	0	0.167	7	0	0
Bivalvia veliger	0.5		0	43	0	0.167	7	0	0
Calanus C1–C4	1–2.5	2	0	100	0	35.56	1488	0	0
Calanus finmarchicus	3	2	68	100	2.74	14.75	617	3.45	0.9
Calanus glacialis	4	3	94	38	23.96	1.219	51	30.13	11.8
C. glacialis	5	4.5	94		19.04	0		23.94	14.1
C. glacialis	6	7.8	87		9.27	0		11.65	11.9
Calanus hyperboreus	7	9	70	62	7.19	0.120	5	9.03	10.6
C. hyperboreus	8	12	66		4.27	0		5.36	8.4
C. hyperboreus	9	13	49		3.07	0		3.86	6.6
C. hyperboreus	10	14	45		2.03	0		2.55	4.7
C. hyperboreus	11	18	43		0.41	0		0.52	1.2
Cirripedia larvae	1.5		0	5		0.120	5	0	0
Copepoda nauplii	0.75		0	86		3.944	165	0	0
Decapoda larvae	10		0	14		0	0.01	0	0
Echinodermata larvae	0.5		0	48		0.765	32		0
Eupagurus pubescens larvae	6	5.3	57		11.19	0		14.06	9.8
Gamarellus homari	5	4	2		0.02	0		0.02	0
Harpacticoida	1.5		0	5		0.024	1		0
Hyas sp *megalopa*	6	1.5	4		0.36	0		0.45	0
Hyas sp *zoea*	5	0.9	26		1.05	0		1.32	0.2
Hyperia galba	6	6	15		0.12	0		0.15	0.1
Limacina spp *juvenes*	2.5			52		0.263	11		0
Microcalanus spp.	0.75			14		0.191	8		0
Oithona atlantica	1.5			33		3.824	160		0
Oithona similis	1.5			95		30.378	1271		0
Oncaea borealis	0.75			5		5.975	250		0
Ostracoda	1.5			5		0.024	1		0
Pandalus borealis larvae	8	5.3	70		9.73	0		12.23	8.5
Paraeuchaeta norvegica	5.5			19		0.120	5		0
Pisces larvae n.d.	15	20	6		0.12	0		0.15	0.4
Pisces larvae n.d.	20	30	11		0.1	0		0.13	0.5
Polychaeta larvae	1.5			14		0.167	7		0
Pseudocalanus spp.	2			90		2.223	93		0
Sabinea septemcarinata larvae	12	8	47		2.52	0		3.17	3.3
Sagitta elegans	38	18	2	33	0.02	0.005	0.2	0.02	0.1
Synopiidae n.d.	6	6	2		0.02	0		0.02	0.0
Themisto abyssorum	6	3.7	32		0.46	0		0.57	0.3
T. abyssorum	8	8	21	14	0.58	0.0002	0.01	0.72	0.8
T. abyssorum	10	14.6	15		0.19	0		0.23	0.5
T. abyssorum	12	23.8	2		0.02	0		0.02	0.1
Themisto libellula	8	6.9	9		0.07	0		0.09	0.1
T. libellula	10	12.9	4		0.05	0		0.06	0.1
T. libellula	12	21.5	21		0.17	0		0.21	0.6
T. libellula	14	33.5	13		0.2	0		0.25	1.1
T. libellula	16	48	9		0.14	0		0.17	1.1
T. libellula	18	67.3	4		0.03	0		0.04	0.3
T. libellula	20	90.6	0		0	0		0	0
Thysanoessa inermis	14	30	4	14	0.08	0.002	0.1	0.11	0.4
T. inermis	18	50	9		0.08	0		0.11	0.7
T. inermis	20	80	4		0.08	0		0.11	1.1
Thysanoessa longicaudata	12	50	6		0.64	0		0.81	100.1
Together							4184		
Calanus in total			100	100	71	51.6	2161	89	69
Decapods larvae in total			70	14	25	<0.1	0.01	93	22
Euphausiids in total			15	14	1	<0.1	0.1	14	2

Little auks distribution at sea

The foraging little auks were mainly distributed within the 100-m isobath around the island, with a majority of the birds located to the northwest of the island. The distribution of little auks coincides with the distribution of cold Svalbardbank water and only a few birds were located in Atlantic water (Fig. 1).

Food of the little auks

Food content analysis is presented in Table 1. Food consisted almost entirely of pelagic crustaceans, mainly copepods (71% of items) of which almost all were older stages of *Calanus glacialis* copepodites. Next in numerical importance were decapod larvae (25%). Other taxa, such as hyperiid amphipods and euphausiids, constituted less than 2% of the food items. In terms of weight, both decapod larvae (22%) and amphipods (5%) made significant contributions, but copepods still made up over 69% of the food biomass. The length frequency of major little auk food items is presented in Fig. 2. The dominant group was formed by 3- to 5-mm-long copepods, followed by 5- to 7-mm-long *Hyas* crab larvae and 10- to 11-mm-long *Sabinea* shrimp larvae. Amphipods and euphausiids occurred mainly in the 12- to 16-mm length class.

Discussion

The minimal length of little auk prey items found was 3 mm, which is apparently the lower size limit of its prey. A similar minimal size has been reported by Bradstreet (1982); Bradstreet and Brown (1985) and Mehlum and Gabrielsen (1993). The food of little auks from the Bjornoya population is similar to that found on Spitsbergen (Stempniewicz 1980; Mehlum and Gabrielsen 1993) and Franz Josef Land (Węsławski et al. 1995). At these localities large copepods (*Calanus glacialis* and *C. hyperboreus*) made up the bulk of biomass and number of items, while *C. finmarchicus* have been found only occasionally. Our findings on caloric values are in

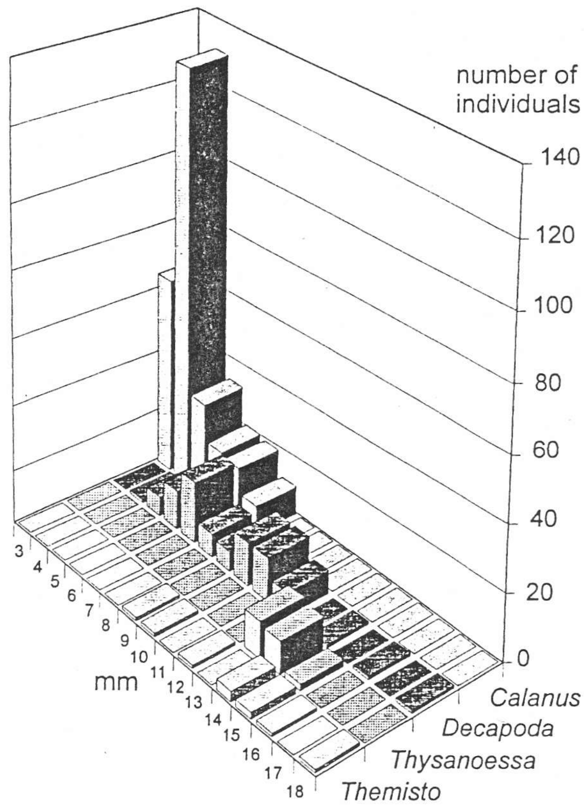

Fig. 2 Length frequency of the little auk prey items from Bjørnøya area (food samples)

Table 2 Characteristics of different size classes in mesozooplankton collected west from Bjørnøya, in July 1995 (six vertical hauls of BONGO net, 50-m depth to the surface)

Size class (mm)	Density (ind/m^3)	Ind ww (mg)	Ind. weight SD (%)	Ind. energy (kJ/g dw)	Energy value (kJ/m^3)	Energy share (%)
1	336	0.82	97.6	19.6	2.1	15.3
2	2673	1.01	79.2	27.3	9.6	71.5
3	45	2.92	54.8	23.6	0.4	2.8
4	33	4.7	44.7	24.95	0.5	4.0
5	15	4.9	63.3	17.4	0.0	0.6
6	17	6.24	46.5	16	0.1	0.9
7	11	14.4	34.0	15.9	0.1	0.9
8	9	11.4	63.2	16.6	0.0	0.6
9	8	27.02	77.4	18.4	0.2	1.2
10	7	18.9	53.2	15.6	0.0	0.3
11	2	37.11	83.5	16	0.0	0.3
12	1	39.9	99.5	16	0.0	0.7
13	1			16	0.0	0.3
14	1			16	0.0	0.0
15	1			16	0.0	0.0
		82.5	66.7	16	0.1	0.8
	3160				13.4	99.9

general accordance with data on selected Arctic plankters presented by Percy and Fife (1981), Bradstreet and Brown (1985) and Szaniawska and Wołowicz (1986). Subadult copepods and juvenile fish are reported to have the highest calorie content of the Arctic plankton, and the lowest values were recorded for large amphipods such as *Gammarus wilkitzkii* (A. Szaniawska, unpublished work). There are no published data concerning the species-specific energy content in different *Calanus* species (*C. finmarchicus*, *C. glacialis*, *C. hyperboreus*). However, in the case of sibling species, the energy content increased with the increasing size of an animal (Szaniawska and Wołowicz 1986). The length frequency of plankters presented in Fig. 3 reflects to some extent the methods of sampling. For example, large, fast-swimming plankters are most likely underestimated in samples obtained by using vertical hauls of WP-2 and BONGO nets. Considering the high variability and year-to-year changes of the system, our data concerning plankton biomass and density are similar to those from other studies from these waters (Węsławski and Kwaśniewski 1989; Kwaśniewski 1995; Hirche and Kwaśniewski 1997). It is also evident that, in summer, the plankton biomass is dominated by small items below 1 mm in length (Kwaśniewski 1995; present study). This explains why waters rich in plankton biomass do not necessarily mean abundant feeding grounds for the little auk. Two northern little auk populations inhabit areas with Arctic water masses (Franz Josef Land) or close to the polar fronts (Spitsbergen), where large copepods prevail (Kwaśniewski 1995; Koszteyn and Kwaśniewski 1992). Bjørnøya lies on the frontal zone of warm Atlantic water, and cold Svalbardbanken water. The high biomass of summer plankton in this region is composed mainly of small species, with large copepods not exceeding 2% of items. This is contrary to the area northeast from Bjørnøya, where large copepods prevail (Tande 1989; Węsławski et al., in press 1998). Little auks select their prey by sight, and apparently consider mainly the size and density of the available food items. A bird taking prey of a given size class, e.g. 2–3 mm, may get either high calorie *Calanus* or low calorie decapod larvae of the same size. By taking prey of 1-to 2-mm size, a bird risks high differentiation of prey weight (weight SD exceeds 70% in this size class): if catching a prey of 3–4 mm the risk is lower (weight SD 40–50%). In large size classes, the risk of their low weight is again high; for example, a class of 11–12 mm contains both fat amphipods and lean appendicularians (weight SD is over 80%). To collect a food equivalent of 100 kJ, which is about half of the little auk's daily energy requirement (Mehlum and Gabrielsen 1996), a bird should catch some 60,000 items of less than 1-mm size, or 6000 items of 4-mm size. The same difference is observed in the volume of water containing 100 kJ of plankton. Small plankters are numerous, and a size class of 3–4 mm makes 100 kJ quickly in 90–100 m^3 of water. Large plankters are more dispersed, and to get 100 kJ from 15-mm-long *Themisto*, a bird would have to sample 700 m^3. The difference found in the plankton composition in waters west of Bjørnøya, and in the little auk diet suggests that birds from the Bjørnøya population utilise the feeding grounds to the northeast, which are apparently more abundant in large plankters. The predominance of *Calanus glacialis* and the frequent presence of *Themisto libellula* in the food indicates Arctic water mass, occurring northeast from Bjørnøya (Grainger 1963; Tande 1989; Węsławski and Kwaśniewski 1989). The distribution of the little auks foraging around Bjørnøya, with the highest concentration northeast from the island, confirms this suggestion.

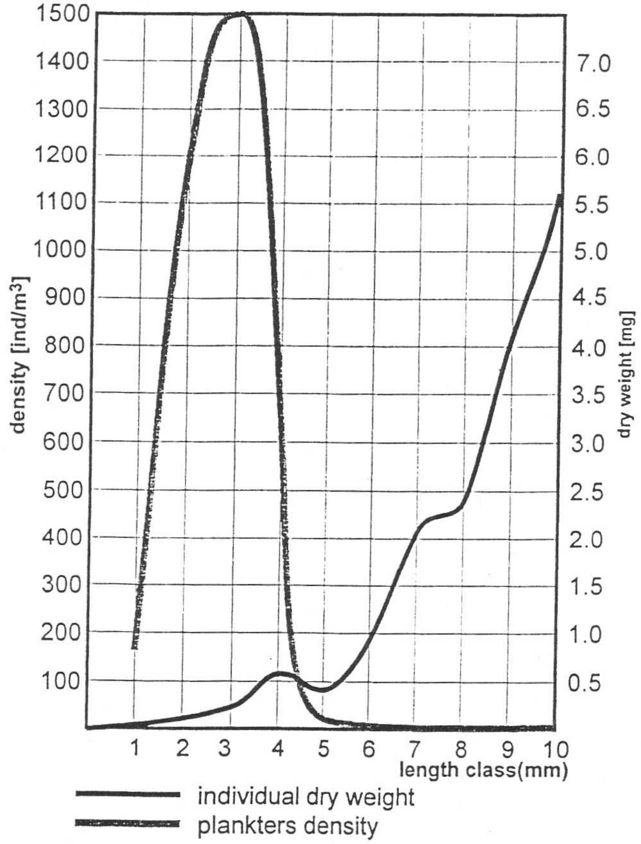

Fig. 3 Relation of plankters individual length/weight to their density (July, Bjornoya shelf)

Conclusions

During the nesting period, little auks from Bjørnøya take mainly the same type of food as birds from more northern populations.

A prey size class of 3–6 mm is the optimal prey group considering its abundance/weight relation.

Little auks from Bjørnøya forage mainly northeast from the island, since the plankton to the west-southwest is dominated by small organisms.

Calanus glacialis, known as the indicator of the presence of Arctic waters, constitutes the cardinal part of the little auks' prey. The sibling Atlantic species, *C. finmarchicus*, is almost absent in the diet, probably because its small size makes feeding unprofitable. An increasing inflow of Atlantic waters into northern Norwegian and Barents Seas, related to a gradual climate warming (Taylor and Stephens 1980), may lead to a decrease of Arctic species in the zooplankton community, leading to a deterioration of the little auk feeding grounds near Bjørnøya, and thereby decreasing the population inhabiting Bjørnøya. A similar phenomenon took place in the nineteenth century, after the end of the "Little Ice Age", when little auks nesting on Iceland abandoned their colonies following the shift in sea currents and plankton dispersal (Nettleship and Evans 1985).

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