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## Summer food resources of the little auk, *Alle alle* (L.) in the European Arctic seas

**ABSTRACT:** Seabird counts were performed during seven summer cruises of *r/v Oceania* to the Norwegian and Greenland seas between 1989 and 1995. Little auk (*Alle alle*) was one of the most numerous seabirds encountered. Biomass of the plankters which consisted little auk food ranged from 0.1 to more than 1g wet weight per m<sup>3</sup> in surface sea layer in the area between 74°N and 78°N and 10°E to 20°E. Seabird concentrations ranged from 0 to more than 4000 per km<sup>2</sup>. Atlantic (Norwegian Sea) plankton with high biomass per water volume unit was dominated by small organisms (mainly *Calanus finmarchicus* copepodites). Also fjordic (Spitsbergen) plankton, although abundant, consisted mainly of organisms less than 3 mm in length (mainly *Pseudocalanus acuspes*). On the contrary, Arctic (Barents Sea) plankton was of low total biomass, but with a considerable proportion of organisms over 3 mm in length (mainly *Calanus glacialis*). We assume that little auks graze 2 to 4% of yearly zooplankton production (6 to 12% of standing stock) in the most frequently visited feeding grounds. On average about 1% of the standing zooplankton stock was estimated as little auk consumption in the studied area.

**Key words:** Arctica, plankton, seabirds, food web.

### Introduction

Little auk, *Alle alle* (L.) is the most numerous planktivorous seabird in the Atlantic sector of the Arctic (Nettleship and Evans 1985, Mehlum and Bakken 1994). Its population in the North-East Atlantic has been estimated at 35 million individu-

als in older surveys (Freuchen and Salomonsen 1958) or at 2 mln in our study area (Norderhaug *et al.* 1977, Brown 1984, Mehlum and Bakken 1994). Regardless of the accuracy of the population estimates, the little auk most likely constitutes an important link in the pelagic food web of the area. The feeding ecology of the European little auk has been studied extensively at Spitsbergen (Norderhaug *et al.* 1977, Stempniewicz 1980, Lonne and Gabrielsen 1992, Mehlum and Gabrielsen 1993) in its northernmost locality at Franz Josef Land (Węśławski *et al.* 1994), as well as in the southernmost area at Bjornoya (Węśławski *et al.* 1999). In the investigated area, little auks have the opportunity to feed on different plankton communities, since at least three different water masses are to be found there. The remains of Coastal Norwegian Waters, the cold Arctic waters of the Barents Current, and the warmest of European Arctic waters from the North Atlantic Current are observed in the region (Lee 1952, Tantsiura 1959, Loeng 1991). Each of these waters is characterised by distinct plankton communities (Kwaśniewski 1994), thus providing different feeding conditions for little auks. Furthermore, the Barents Sea and European Arctic waters in general are regarded as a very unstable system, with pronounced year-to-year changes (Sakshaug 1992, 1997).

The aim of the present paper was to describe summer food resources for little auks as well as to assess their role as zooplankton grazers in the study area.

## Material and methods

Plankton data are based on the collection of samples from seven *Oceania* cruises to Spitsbergen in 1987–1995, as well as from the cruise of *Lance* to the North West Barents Sea in 1992. Part of the data on plankton has been presented in other contexts in earlier publications (Węśławski *et al.* 1991, Kwaśniewski 1994, Koszteyn *et al.* 1995). Seabird distribution data have been collected during *Oceania* cruises in 1991–1995 (Fig. 1) and were preliminarily elaborated as source materials (Malinga and Stempniewicz 1996). Methods applied in the zooplankton and seabirds estimates have been described in detail in the papers cited above. In general, seabirds were observed according to the method recommended by Tasker *et al.* (1984). Plankton was collected with vertical hauls of a WP-2 net of 200  $\mu\text{m}$  mesh size. Plankton data from the surface water layer of 30 to 0 m are presented in this study, since this is most likely the depth diving limit for little auks (Bradstreet and Brown 1985). Measurements of the calorific value were conducted by bomb calorimetry by Dr. Monika Normant (University of Gdańsk). The length of zooplankters was measured from the tip of the head to the end of the telson (end of furca in the case of copepods, end of fins in fishes and arrow worms), excluding setae or spines. Wet weight was obtained from the formaline preserved materials, after blotting the animal on filter paper. Dry weight was measured after 24 hours of drying at 60°C. Ash-free dry weight was established after burning the sample at

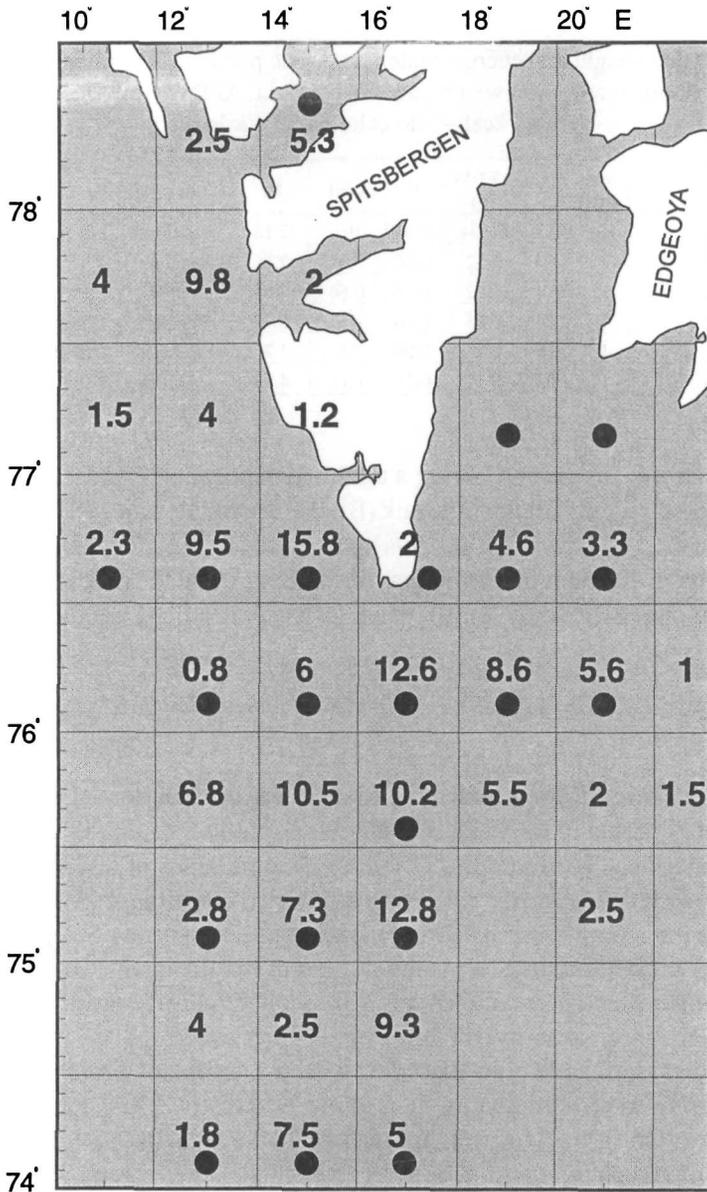


Fig. 1. Study area, with geographical grid and number of observation hours for each cell of the grid. Zooplankton sampling stations marked with large dots.

450°C. Weight measurements were performed with 0.2 mg accuracy. In the case of minute animals having a mass below 1 mg, ten or twenty specimens were weighed together. For all size classes, a general relation between weight, energy, and carbon content was established, as presented in Table 1. It should be noted, that formaline weight usually differs about 10% from fresh weight.

Table 1  
Relation between weight and energy content in Arctic plankton according to different authors. Abbreviations: ww – wet weight, dw – dry weight, AFDW – ash free dry weight, C – carbon, kcal – kilo calories, kJ – kilo joule.

object	ww (g)	dw (g)	AFDW (g)	C	kcal	kJ	area	author
zooplankton	1	0.13	0.104	0.05	0.5	2.18	N. Atlantic	Mullin 1969
zooplankton	1	0.14	0.12	0.06	0.68	2.86	Resolute	Welch <i>et al.</i> 1992
zoopl. 3–10 mm class	1	0.14	0.12	0.06	0.64	2.65	Svalbard	present work
little auk food	1	0.24	0.15	0.16	1.62	6.72	Svalbard	Gabrielsen <i>et al.</i> 1991
Copepoda	1	0.15	0.14	0.09	0.9	3.76	N. Pacific	Omori 1969
<i>Themisto libellula</i>	1	0.23	0.19	0.11	1.13	4.73	Arctic	Percy and Fife 1981

All planktonic organisms having a total length between 2 and 15 mm were regarded as potential prey for the little auk (Bradstreet and Brown 1985, Mehlum and Gabrielsen 1993, Węśławski *et al.* 1994). Since the pre-breeding and autumn feeding birds have a different diet from that of summer, our data are based on the collection from one month only (July), when little auk nestlings are fed.

## Results

### Characteristics of the planktonic taxa and size structure of communities.

— All items reported in the cited literature as the little auks food items were collected in our zooplankton samples (Table 2). Size fractions of less than 2 mm (regarded as “unedible” *i.e.* too small for the little auks) constituted 65% of the fjordic plankton biomass (expressed in  $\text{kJ}\times\text{m}^{-3}$ ), 24% of the Norwegian Sea plankton, and less than 3% of the Barents Sea plankton. Length frequency of plankters found in the three above-mentioned samples sets is presented in Fig. 2. It shows that fjordic samples were dominated by the smallest size classes of 1 to 2 mm (mainly *Pseudocalanus* spp.) attaining  $3\text{kJ}\times\text{m}^{-3}$ , with a significant proportion of large *Sagitta elegans arctica* amounting to  $2\text{kJ}\times\text{m}^{-3}$ . Items of 3 to 4 mm length were found more often in the Norwegian Sea samples (consisting mainly of *Calanus finmarchicus*), reaching over  $5\text{kJ}\times\text{m}^{-3}$ . The Barents Sea plankton was dominated by large organisms 4–6 mm in length (mainly *Calanus glacialis*). The size fraction between 5 and 10 mm consisted mainly of decapod larvae and hyperiid amphipods of relatively low energy content (Table 2).

**Density and biomass of the surface water plankton.** — The Barents Sea samples were of an order of magnitude poorer in biomass and density when compared with fjordic and Norwegian Sea material (Table 2). The energy content of Barents Sea plankton did not exceed  $3.75\text{kJ}\times\text{m}^{-3}$ , while fjordic plankton attained on average  $6.9\text{kJ}\times\text{m}^{-3}$  and that of Atlantic waters over  $11\text{kJ}\times\text{m}^{-3}$  (Table 2). Bio-

Table 2

List of planktonic taxa from upper 30 m, selected according to the size class. Abbreviations: n – number of samples; SD – standard deviation; dw – dry weight; ww – wet weight; CI–CVI – copepodite stages; [m] – males; [f] – females.

size class mm	T A X O N	ind. ww		energy content kJ × g dw <sup>-1</sup>	density ind. × m <sup>-3</sup>		
		mean mg	SD		Norw. Sea n = 25	Barents Sea n = 9	Fjords n = 14
1	2	3	4	5	6	7	8
<1.1	<i>Bosmina</i> sp. Bryozoa larvae Calanoida nauplii <i>Calanus finmarchicus</i> (Gunner) CI Cirripedia cypris Cirripedia nauplii <i>Evadne nordmanni</i> Loven Harpacticoida nauplii <i>Idyaea</i> sp. Isopoda non det. <i>Metridia longa</i> (Lubbock) CI–II <i>Microcalanus pusillus</i> Sars <i>Microsetella norvegica</i> Boeck <i>Nebalia bipes</i> (Fabricius) <i>Oithona antarctica</i> Farran <i>Oithona similis</i> Claus <i>Oncaea borealis</i> Sars Ostracoda <i>Podon leucartii</i> Sars <i>Pseudocalanus</i> spp. CI–CIII <i>Temora longicornis</i> (Müller)	0.26	0.79	19.6	25.15	494	4 083
1.1–2	<i>Calanus glacialis</i> Jashnov CI–II <i>Acartia longiremis</i> Lilljeborg <i>Calanus finmarchicus</i> (Gunnerus) CII–III <i>Acartia clausi</i> Giesbrecht <i>Pseudocalanus acuspes</i> (Giesbrecht) CIV–CVI [m] <i>Pseudocalanus minutus</i> (Krøyer) CIV–CVI [m] <i>Bradyidius similis</i> Sars CI–CIII <i>Centropages hamatus</i> (Lilljeborg) <i>Centropages typicus</i> Krøyer <i>Metridia longa</i> (Lubbock) CIII–CIV Gastropoda larvae <i>Paracalanus parvus</i> (Claus) <i>Pareuchaeta norvegica</i> (Boeck) CII <i>Scolecithricella minor</i> (Brady) CIII–CVI <i>Clione limacina</i> veliger <i>Limacina helicina</i> (Phillips) veliger Bivalvia (Phillips) veliger Echinodermata larvae <i>Oikopleura</i> sp. <i>Fritillaria borealis</i> Lohman <i>Calanus hyperboreus</i> Krøyer CII Harpacticoida non det.	0.46	0.77	25.7	950	40	801

Table 2 – *continued.*

1	2	3	4	5	6	7	8
2.1-3	<i>Calanus glacialis</i> Jashnov CIII–CIV <i>Candacia</i> sp. <i>Calanus finmarchicus</i> (Gunnerus) CIV <i>Bradyidius similis</i> (Sars) CIV–CVI <i>Metridia longa</i> (Lubbock) CV <i>Metridia lucens</i> Boeck <i>Pareuchaeta norvegica</i> (Boeck) CIII <i>Limacina retroversa</i> (Fleming) Polychaeta larvae	1.98	1.61	23.6	394	11	113
3.1-4	<i>Calanus hyperboreus</i> Krøyer CIII <i>Calanus finmarchicus</i> (Gunnerus) CV–CVI [m] <i>Heterorhabdus norvegicus</i> (Boeck) CIV–CVI <i>Limacina helicina</i> (Phillips) Polychaeta non det. <i>Metridia longa</i> (Lubbock) CVI <i>Pareuchaeta norvegica</i> (Boeck) CIV <i>Pleuromamma</i> sp. <i>Eupagurus pubescens</i> Krøyer zoea <i>Hyas</i> sp. zoea	4.04	2.1	25	888	4	32
4.1-5	<i>Calanus hyperboreus</i> Krøyer CIV <i>Calanus glacialis</i> Jashnov CV	4.89	3.1	17.4	57	44	18
5.1-6	<i>Calanus hyperboreus</i> Krøyer CV <i>Calanus glacialis</i> Jashnov CVI [f] <i>Calanus glacialis</i> Jashnov CVI [m] <i>Pareuchaeta norvegica</i> (Boeck) CV <i>Eupagurus pubescens</i> Krøyer zoea <i>Clione limacina</i> (Phillips)	6.24	2.9	16	7	10	0
6.1-7	<i>Thysanoessa inermis</i> Krøyer furciliae <i>Thysanoessa</i> sp. furciliae <i>Thysanoessa</i> sp. calyptopis Hyperiididae juv. non det.	14.4	4.9	15.9	0	0	1
7.1-8	<i>Calanus hyperboreus</i> Krøyer CVI [f] <i>Onisimus</i> sp. juv. Decapoda larvae non det.	11.4	7.2	16.7	0.0	0.4	0.0
8.1-9	<i>Themisto abyssorum</i> (Boeck)	27.2	20.9	18.4	0.0	0.1	0.0
9.1-11	<i>Eukrohnia hamata</i> Mobius Chaetognatha non det. <i>Themisto</i> sp. juv. <i>Hyperia medusarum</i> (Müller)	18.92	10.1	15.6	0	0	0.1
11.1-12	<i>Themisto libellula</i> (Mandt)	39.86	39.7	17	0	0.1	0.0
12.1-17	<i>Thysanoessa inermis</i> (Krøyer) <i>Thysanoessa</i> sp. Pisces larvae	82.5	55	17	0	0	0.1

Table 2 – continued.

1	2	3	4	5	6	7	8
17.1-20	<i>Gammarus wilkitzkii</i> Birula <i>Sagitta elegans</i> Aurivillius	55.98	25.7	17	0.2	0.9	8.4
	total density [ $n \times m^{-3}$ ]				3 609	606	5 059
	mean energy [ $kJ \times m^{-3}$ ]				11.3	3.8	6.9
	2-20 mm size class energy [ $kJ \times m^{-3}$ ]				8.5	3.7	2.4
	% of energy stored in large plankters				76	97	35
	total wet weight [ $g \times m^{-3}$ ]				3.2	0.6	2.3

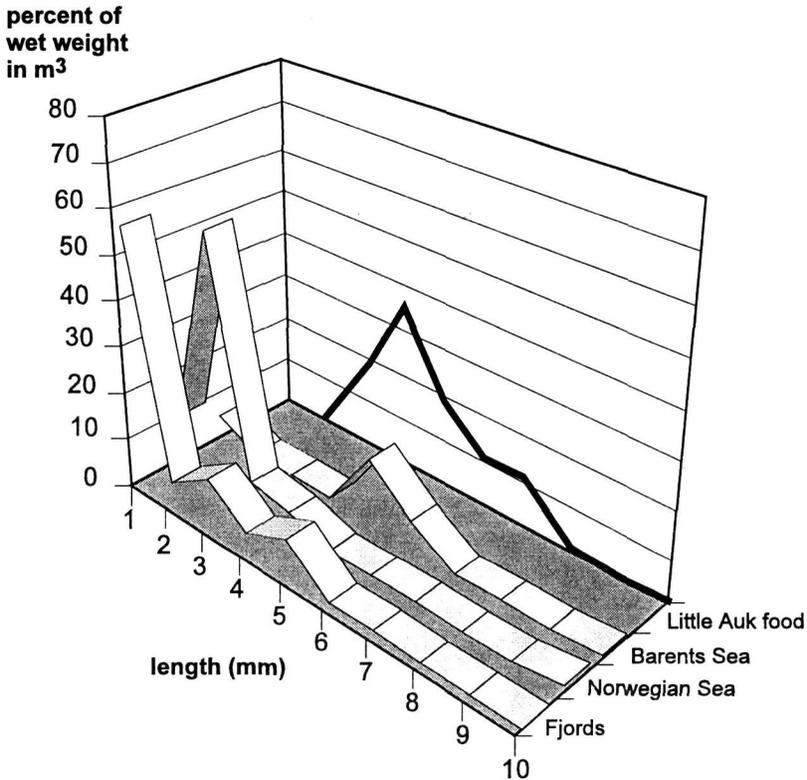


Fig. 2. Length frequency distribution of plankters in surface communities and in little auk food.

mass of the food items ranged from below  $0.1g \times m^{-3}$  to over  $1g$  wet weight per  $m^3$ . In terms of food items biomass the richest areas were along the South-West Spitsbergen coast (Fig. 3).

***Calanus finmarchicus* / *C. glacialis* ratio.** — Numerically the most important zooplankton items were two sibling species, Atlantic *C. finmarchicus* and Arctic *C. glacialis*. Their distribution reflects the composition of the water masses. The

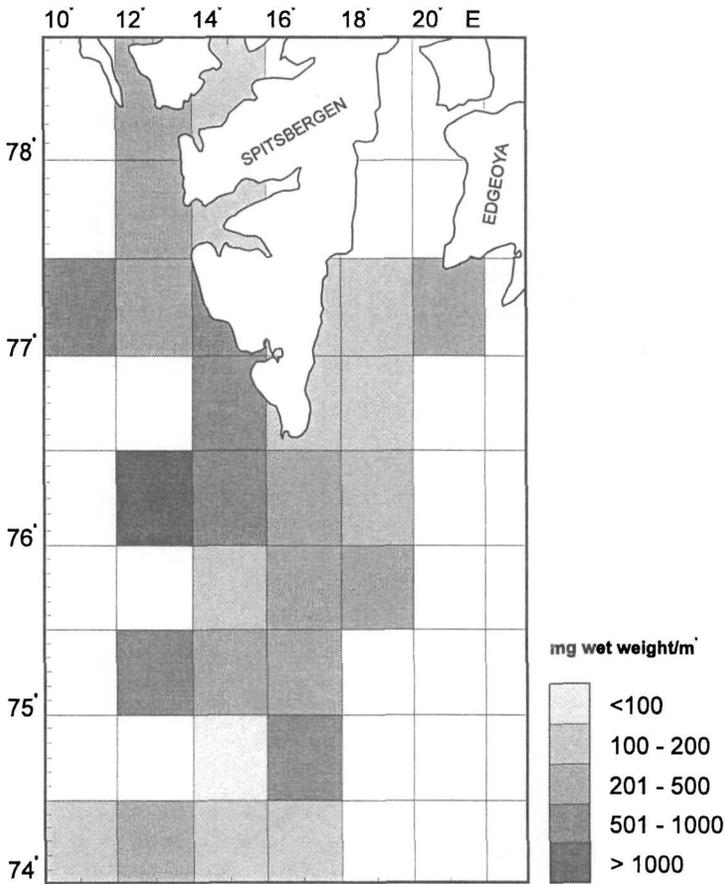


Fig. 3. Distribution of little auk's food items biomass in 0–30 m water layer. Data compiled from July, 1987–1993.

larger species (*C. glacialis*) prevailed in fjords and in eastern localities (Barents Sea), while western and southern stations (Norwegian Sea) were dominated 100% by *C. finmarchicus* (Fig. 4). The size of developmental stages presented in Table 2 shows that a length over 2 mm was attained by copepodites IV and V and adults of *C. finmarchicus*, as well as copepodit +III and older stages of *C. glacialis*. None of the *C. finmarchicus* reached 4 mm length, but *C. glacialis* copepodite V and adults exceeded that size.

**Little auk density at sea.** — Counts performed during four nesting seasons in July are summarized in Fig. 5. The largest concentrations of little auks were found at the entrances to Hornsund and Isfjorden as well as around Sorkapp (from 500 to over 1000 birds per km<sup>2</sup>). Low densities (below 100 birds per km<sup>2</sup>) were observed near Bjornoya. Maximal concentrations encountered in small spots exceeded 4000 birds×km<sup>-2</sup>.

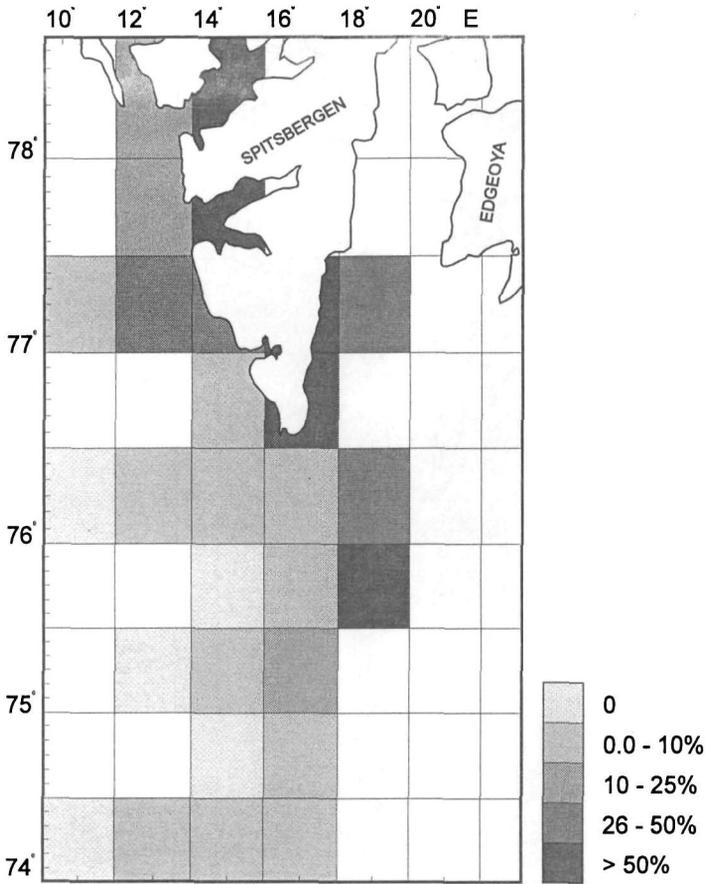


Fig. 4. Percent share of *Calanus glacialis* to other *Calanus* species in the surface waters in surface water layer. Data compiled from July, 1987–1993.

## Discussion

**Characteristics of the planktonic taxa .** — Data on calorific values of selected Arctic plankton species have been presented by Omori (1969), Williams and Robins (1980), Percy and Fife (1981), Szaniawska and Wołowicz (1986), Wołowicz and Szaniawska (1986), and Welch *et al.* (1992). As summarized in Table 1 these are in general accordance with our findings, performed both for particular species as well as for a random selection of size fractions. Subadult copepods and juvenile fish are reported as the richest in calories in the Arctic plankton, while low values (below 18 kJ g dw) were measured for large amphipods like *Gammarus wilkitzkii*, or *Themisto libellula* (Williams and Robins 1980, Percy and Fife 1981, Szaniawska, *unpubl.*). It was also reported that Arctic plankton consists of larger animals when compared with plankton from boreal waters [see Dunbar (1968) for general discussion, and

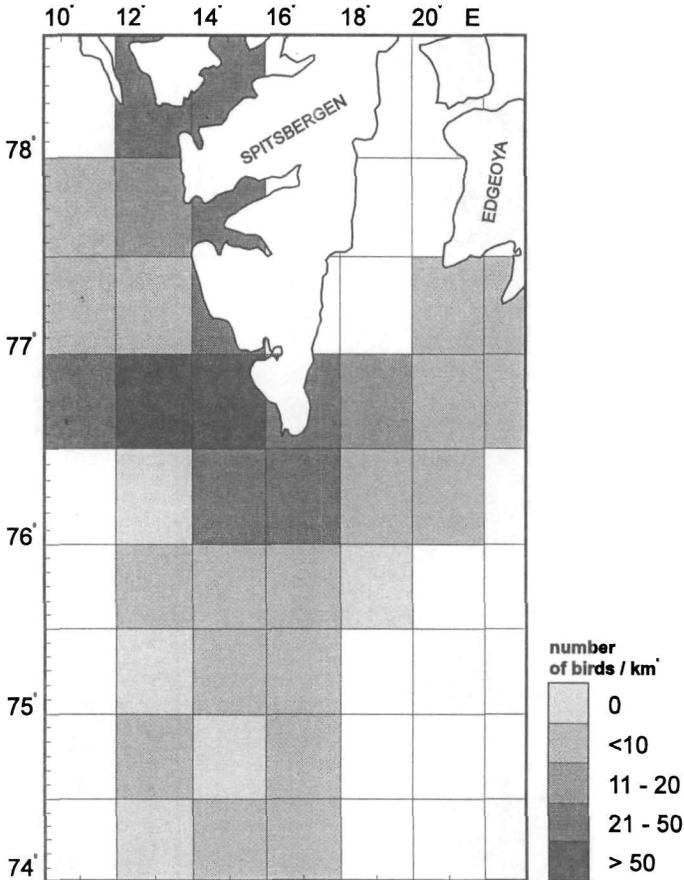


Fig. 5. Mean density of little auks at sea (data from July 1991–94).

Kwaśniewski (1994) for our study area]. *C. glacialis* is characteristic of cold, Arctic waters (Jashnov 1961, Grainger 1963). Its copepodite III and older stages exceed 2 mm in length (Koszteyn and Kwaśniewski 1992). Coastal plankton from Franz Josef Land at 80°N was dominated by the largest calanoids (*C. glacialis* and *C. hyperboreus*) and accompanied by ice fauna (Koszteyn and Kwaśniewski 1992, Węslawski *et al.* 1994). Fjordic plankton was dominated in our samples by small *Pseudocalanus* species and Cirripedia larvae, both not exceeding 2 mm in length. That size fraction is typical of the plankton of Nordic fjords (Matthews and Heimdal 1980). Atlantic plankton in the area usually contained a large proportion of 2–4 mm long *C. finmarchicus* (Diel 1991, Mumm 1993).

**Plankton concentrations.** — Recent data on plankton concentrations in the investigated area are surprisingly scarce. Some older materials may be found in the papers by Abramova (1956) and Lie (1965). They give an average value of plankton density exceeding over 0.8 g ww×m<sup>-3</sup> in the N. Atlantic waters surrounding

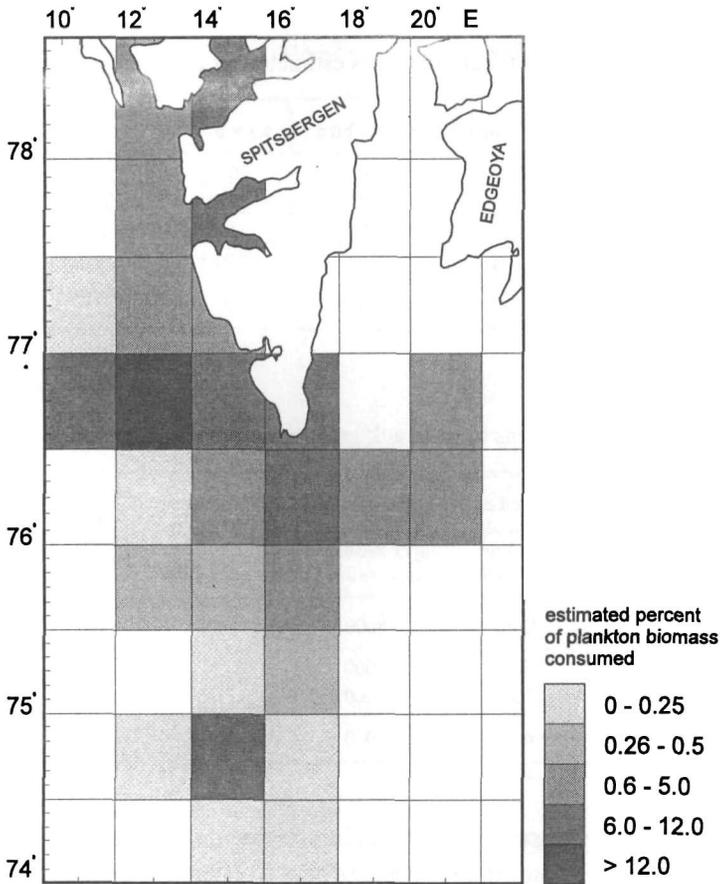


Fig. 6. Estimated consumption of little auks calculated for 60 days and 30 g dry weight of food daily, as percent of plankton biomass in 0–30m water layer .

Spitsbergen. To the west of the studied area there is a number of data on Greenland Sea plankton (Diel 1991, Mumm 1993, Mumm *et al.* 1998). Its average density in the surface layer ranges from 0.5 to 1g  $\text{ww} \times \text{m}^{-3}$ . Similar values (from 0.1 to 1g  $\text{ww} \times \text{m}^{-3}$ ) are reported from Spitsbergen fjords (Kwaśniewski 1990, Kwaśniewski 1994, Węśławski and Kwaśniewski 1990, Węśławski *et al.* 1994). Low biomass (0.15g  $\text{ww} \times \text{m}^{-3}$ ) of cold, Arctic waters plankton was reported for Northeast Greenland coastal waters (Hirche and Kwaśniewski 1997). For the Barents Sea, the general production value of 8 g zooplankton carbon  $\times \text{m}^{-2} \times \text{year}^{-1}$  is given by Sakshaug (1992). Mumm *et al.* (1998) reports 2 to 3 g  $\text{dw} \times \text{m}^{-2}$  in the upper 100 m of the West Spitsbergen Currents, which might be transferred to 0.14 to 0.21 g  $\text{ww} \times \text{m}^{-3}$  in surface waters. Lowry (1993) reports 0.3 to 2.3 g  $\text{ww} \times \text{m}^{-3}$  in surface summer plankton of Baffin Bay. Considering the high variability and year-to-year changes in the system, it may be stated that our data concerning plankton biomass and density fit in the ranges given by other authors.

Table 3

Little auk energy requirements as estimated by different authors.

daily consumption % of body weight	g dw × bird <sup>-1</sup>	g ww × bird <sup>-1</sup>	kJ × bird <sup>-1</sup>	author
80%	31.5	131.3	696	Gabrielsen <i>et al.</i> 1991
60%	14	99.2	214	Weich <i>et al.</i> 1992
40%	8.96	64	138	Hunt <i>et al.</i> 1991
32%	7.11	50.77	109.5	Schneider <i>et al.</i> 1967
25%	5.6	40	86	Stempniewicz and Węśławski 1992

Table 4

Estimations of little auk grazing on zooplankton.

assumed density of birds at sea ind. × km <sup>-2</sup>	individual daily food intake g ww × bird <sup>-1</sup>	calculated daily food intake from km <sup>2</sup> kg ww × km <sup>-2</sup>	mean food items biomass layer 0–30 mm kg ww × km <sup>-2</sup>	food intake in July from km <sup>2</sup> kg ww × month <sup>-1</sup>	amount of biomass removed in July %	author
30	50.8	1.46	8000	45	0.6	Joiris <i>et al.</i> 1996
500	111	55.5	20000	1721	8.6	present paper
50	111	5.55	20000	172	0.9	present paper
50	131.3	6.6	20000	205	1.0	Gabrielsen <i>et al.</i> 1991

**Little auk density at sea.** — It should be stressed that the data presented in Fig. 5 are extrapolated data from small squares of actual observations to large ones in our grid. Hence the numbers given should be treated as an indication of the most commonly encountered density in any given square and not as an exact census of seabirds in each 50 × 50 km square. Total seabird Svalbard population is estimated to be ca. 2 mln little auks (Mehlum and Bakken 1994). The population from Hornsund constitutes some 40% of that number (Isaksen and Bakken 1995). Extensive seabird counts performed in 1986–1990 by Norsk Polarinstittutt (Bakken and Mehlum 1988, Isaksen & Bakken 1995) report mean concentrations of 50 little auks × km<sup>-2</sup> at the most densely visited areas near South West Spitsbergen. Surveys by Dutch ornithologists in 1980–1990 report 10 little auks × km<sup>-2</sup> in the same area, however dense patches of up to 1000 birds × km<sup>-2</sup> were also noted (Camphuysen 1993).

Data from the central and northern Greenland Sea indicating little auk concentrations of 65 to 205 birds × km<sup>-2</sup> was published by Joiris (1992). Dense concentrations reaching 1000 birds × km<sup>-2</sup> have also been noted off the Norwegian coast (Follestad 1990). The little auk is known for its strong migratory behaviour and during the postbreeding season it occupies different areas of the sea (Lovenskjoeld 1964). High little auk concentrations at sea have also been reported on the eastern border of our study area (Isaksen and Bakken 1995). The differences in seabird densities are

caused by the method of data extrapolation from actual observation areas to square grids on the map (Fig. 5) as well as the year-to-year differences in seabird distribution. Apparently, little auks are distributed along the colonies locations at sea (Camphuysen 1993, Isaksen and Bakken 1995). Auks can fly long distances daily for food – up to 150 nautical miles, towards the pack ice edge (Lovenskjold 1964, Norderhaug *et al.* 1977, Joiris 1992, Mehlum and Gabrielsen 1993, Mehlum 1997).

**Estimation of plankton consumption by little auk.** — The daily food intake of little auks is presented very differently by different authors (Table 3). We have adopted an equivalent of 60% mean little auk body weight (after Welch *et al.* 1992). Observations from Spitsbergen and Bjornoya (Stempniewicz 1980, Stempniewicz and Jezierski 1987, Stempniewicz and Węśławski 1992) indicate that during the chick-feeding period some 30 g wet weight of plankton is delivered to the nest daily. Gabrielsen *et al.* (1991) estimated the food mass delivered to chick each day as 50 g ww. Considering 60 days of intensive feeding and multiplying this by the mean number of birds feeding at sea on a given grid (Fig. 1), we may estimate the food mass taken by the little auks each season (non gelatinous plankton 2 to 15 mm size). Our calculation assumes 99 g ww of plankton eaten by each bird daily (Table 3) plus 30 g of food for chicks collected by some 40 percent of adult birds daily (considering 80% of population as breeding, and two birds feeding one chick). As a result we arrive at 111 g wet weight of plankton taken by an average bird daily (Table 4). This rather conservative figure lies between the low and high values used by other authors, since Gabrielsen *et al.* (1991), estimated the mass of food collected by each breeding pair daily as 313 g ww (2 adults take 131 g each plus 50 g for chick, Table 3). Furthermore, knowing the mass of potential food occurring in a given geographical area, we may estimate the pressure exerted by the little auk on the surface plankton community. The percentage of plankton removed by the little auks from a 0–10 m water layer in July–August is presented in Fig. 6. It shows the highest grazing at the shelf break along West Spitsbergen and around Sorkapp (from 6 to over 12% of food items biomass during the feeding season). The lowest consumption was observed close to Bjornoya (values below 0.25%). Locally, large little auk concentrations amounting to 4000 birds per 1 km<sup>2</sup> may take from 444 kg to 624 kg of surface plankton daily. Considering the rich plankton community presented in Table 2, where 76% of 3.2 g ww plankton biomass were the little auks food items, *i.e.* 2.4 g ww×m<sup>-3</sup> (24000 kg×km<sup>-2</sup> in 0–10 m layer), we arrive at a maximal value of 1.8 to 2.6% of standing stock consumed by the little auks per day.

According to Petersen and Curtis (1980) and Sakshaug (1992) the relation between yearly production and biomass (P/B) in the North Atlantic plankton is 3:1, hence little auks may consume from 2 to over 4% of the zooplankton production in the studied area (6 to 12% of biomass). Other estimations based on different data were presented by Stempniewicz and Węśławski (1992) at 10% of plankton biomass consumed by little auks in the Hornsund area. Food intake by little auks was

estimated in the Central Greenland Sea by Joiris (1992) as 0.46 to 1.46 kg ww  $\times$  km<sup>-2</sup> (Table 4). This is about 1% of the plankton biomass estimated for this area by Hirche and Kwaśniewski (1997). For the whole Barents Sea area the little auk daily consumption is estimated at 210 tons of plankton (Sakshaug 1992) or 0.1% of zooplankton production (calculated from data in Mehlum and Gabrielsen 1993, 1995).

The three water masses (Atlantic, Arctic, fjordic) observed in the investigated area are characterized by different plankton species and size distributions. Atlantic plankton is the richest in biomass, but is represented by relatively small individuals. Arctic plankton has "the most proper" size structure, but low biomass, and fjordic plankton has only 35% of biomass potentially available to little auks (items over 2 mm length). The best feeding grounds occur at the confluence zone of all three water masses.

Assuming the mean number of birds observed at feeding grounds as 100 birds  $\times$  km<sup>-2</sup>, daily food intake per average bird as 111 g wet weight, and 60 days of intensive feeding during the nesting period, the little auks consume 2 to 4% of the yearly zooplankton production (6 to 12% of the standing stock). Welch *et al.* (1992) estimated some 30% of copepods production to be transferred to planktivores in Arctic Canada. Considering the transfer of 50% of zooplankton production to the pelagic carnivores (zooplankton, fish, birds and mammals) in general (Petersen and Curtis 1980) we may conclude that the little auk acts as a very important, plankton predator in the investigated area.

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## References

- ABRAMOVA V.D. 1956. Plankton kak indikator vod razlichnogo proizhozhdenija v morjach severnoj Atlantiki. — Trudy PINRO, 9: 69–92.
- BAKKEN V. and Mehlum F. 1988. AKUP – sluttrapport, sjofuglerundersokelser nord for N 74° (Bjornoya). — Norsk Polarinstittutt Rapportserie, 44: 1–179.
- BRADSTREET M.S.W. and BROWN R.G.B. 1985. Feeding ecology of the Atlantic alcidae. — *In: The Atlantic Alcidae*. Acad. Press, London; 263–318.
- BROWN R.G.B. 1984. Seabirds in the Greenland, Barents and Norwegian seas, February–April 1982. — *Polar Res.*, 2: 1–18.
- CAMPHUYSEN C.J. 1993. Su mmer distribution of seabirds and marine mammals in the Greenland Sea, 1985–1990. — *Sula*, 7: 45–63.
- DIEL S. 1991. On the life history of dominant copepod species (*Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa*) in the Fram Strait. — *Ber. Polarforsch.*, 88: 113 pp.
- DUNBAR M.J. 1968. Polar ecosystems. Study in evolution. — Prentice Hall inc. Inglewood Cliffs NY, 125 pp.

- FOLLESTAD A. 1990. The pelagic distribution of little auk *Alle alle* in relation to a frontal system off central Norway, March/April 1988. — *Polar Res.*, 8: 23–28.
- FRUCHEN P. and SALOMONSEN F. 1958. *The Arctic Year*. — G.P. Putnam's Sons. New York; 440 pp.
- GABRIELSEN G.W., TAYLOR J.R.E., KONARZEWSKI M. and MEHLUM F. 1991. Field and laboratory metabolism and thermoregulation in dovekies (*Alle alle*). — *Auk*, 108: 71–78.
- GRAINGER E.H. 1963. Copepods of the genus *Calanus* as indicators of eastern Canadian waters. — *In: M.J. Dunbar* (ed.), *Marine distribution*. Univ. of Toronto Press; 68–94.
- HUNT G. Jr, Burgeson B. and Sanger G.A. 1981. Feeding ecology of seabirds of the eastern Bering Sea. — *In: D.W. Hood and J.A. Calder* (eds), *The Eastern Bering Sea shelf: Oceanography and resources*. Washington DC, OMPA/NOAA; 629–647.
- HIRCHE H.J. and KWAŚNIEWSKI S. 1997. Distribution, reproduction and development of *Calanus* species in the North East Water in relation to environmental conditions. — *J. Mar. Syst.*, 10: 299–317.
- ISAKSEN K. and BAKKEN V. 1995. Seabird populations in the Northern Barents Sea. — *Medd. om Norsk Polarinstittutt*, 135: 1–134.
- JASHNOV V.A. 1961. Vodnyje massy i plankton. 1. Vidy *Calanus finmarchicus*, *C. glacialis*, *C. helgolandicus* kak indikator y vodnykh mass Atlanticeskogo okeana. — *Zool. Zh.*, 40: 1314–1334.
- JOIRIS C.R. 1992. Summer distribution and ecological role of seabirds and marine mammals in the Norwegian and Greenland seas (June 1988). — *J. Mar. Syst.*, 3: 73–89.
- JOIRIS C.R., TAHON J., HOLSBECK L. and VANCAUWENBERGHE M. 1996. Seabirds and marine mammals in the eastern Barents Sea: late summer at sea distribution and calculated food intake. — *Polar Biol.*, 16: 245–256.
- KOSZTEYN J. and KWAŚNIEWSKI S. 1992. The near shore zooplankton of the Tikhaia Bay (Franz Josef Land) in August 1991. — *Norsk Polarinstittutt Meddelelser*, 120: 23–33.
- KOSZTEYN J., TIMOFFEV S., WĘŚLAWSKI J.M. and MALINGA B. 1995. Size structure of *Themisto abyssorum* Boeck and *Themisto libellula* (Mandt) populations in European Arctic seas. — *Polar Biol.*, 15: 85–92.
- KWAŚNIEWSKI S. 1990. A note on zooplankton of the Hornsund fjord and its seasonal changes. — *Oceanografia*, 12: 7–27.
- KWAŚNIEWSKI S. 1994. Rozmieszczenie mesozooplanktonu w epipelagialu strefy granicznej Morza Norweskiego i Barentsa w okresie letnim. University of Gdańsk, ph.D. thesis, 49 pp.
- LEE A.J. 1952. The influence of hydrography on the Bear Island Cod fishery. — *Cons. Int. Perm. Expl. Mer. Rapp. et Proc. Verb.*, 131: 74–102.
- LIE U. 1965. Quantities of zooplankton and propagation of *Calanus* at permanent stations on the Norwegian coast and at Spitsbergen 1959–1962. — *Fiskeri Direkt. Skrifter Ser. Hav. Undersok.*, 134: 5–19.
- LOENG H. 1991. Features of the physical oceanography. Conditions of the Barents Sea. — *Polar Res.*, 10: 5–18.
- LONNE O.J. and GABRIELSEN G.W. 1992. Summer diet of seabirds feeding in sea-ice-covered waters near Svalbard. — *Polar Biol.*, 12: 685–692.
- LOVENSKJOLD H.L. 1964. Avifauna Svalbardiensis. — *Norsk Polarinstittutt Skrifter*, 129: 500 pp.
- LOWRY L.F. 1993. Foods and feeding ecology. — *In: J.J. Bruns, J.J. Montague and C.J. Cowles* (eds), *The Bowhead whale*; 201–238.
- MALINGA M. and STEMPNIEWICZ L. 1996. Seabirds distribution in the Barents and Greenland Seas, during the summer seasons, 1991–1995. — *In: R.Z. Klekowski and J.M. Węślawski* (eds), Supplement to the "Atlas of Southern Spitsbergen marine fauna". Polish Academy of Sciences, Sopot, 114 pp.

- MATTHEWS J.B.L. and HEIMDAL B.R. 1980. Pelagic productivity and food chains in fjord systems. — *In*: H.J. Freeland, D.M. Farmer and C.D. Levings (eds), *Fjords oceanography*. NATO Conf. Ser. IV, Mar. Sci.; 377–398.
- MEHLUM F. 1997. Seabird species associations and affinities to areas covered with sea ice in the northern Greenland and Barents Seas. — *Polar Biol.*, 18: 116–127.
- MEHLUM F. and BAKKEN V. 1994. Seabirds in Svalbard. Status, recent changes and management. — *In*: D.N. Nettleship, J. Burger and M. Gochfeld (eds), *Seabirds on islands*. Birds Life Conservation Series, 1: 155–171.
- MEHLUM F. and GABRIELSEN G.W. 1993. The diet of high-arctic seabirds in coastal and ice covered, pelagic areas near the Svalbard archipelago. — *Polar Res.*, 12:1–20.
- MEHLUM F. and GABRIELSEN G.W. 1995. Energy expenditure and food consumption by seabird populations in the Barents Sea region. — *In*: H.R. Skjoldal, C. Hopkins, K.E. Erikstad, and H.P. Leinaas (eds), *Ecology of fjords and coastal waters*. Elsevier Sci. BV; 457–470.
- MULLIN M.M. 1969. Production of zooplankton in the ocean: present status and problems. — *In*: H. Barnes (ed.), *Oceanography and Marine Biology, Annual Review*. Allen and Unwin, London; 293–314.
- MUMM N. 1993. Composition and distribution of mesozooplankton in the Nansen Basin, Arctic Ocean during summer. — *Polar Biol.*, 13: 451–461.
- MUMM N., AUEL H., HANSSSEN H., HAGEN W., RICHTER C. and HIRCHE H.-J. 1998 Breaking the ice: large scale distribution of mesozooplankton after a decade of Arctic and transpolar cruises. — *Polar Biol.*, 20: 189–197.
- NETTLESHIP D.N. and EVANS P.G.H. 1985. Distribution and status of the Atlantic Alcidae. — *In*: D.N. Nettleship and T.R. Birkhead (eds), *The Atlantic Alcidae*. Acad. Press, London; 53–154.
- NORDERHAUG M., BRUN M. and MOLLEN G.V. 1977. Barentshavet sjofuglerresurser. — *Norsk Polarinstitutt Meddelelser*, 104: 119 pp.
- OMORI M. 1969. Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. — *Mar. Biol.*, 3: 4–10.
- PERCY J.A. and FIFE F.J. 1981. The biochemical composition and energy content of Arctic Marine Macrozooplankton. — *Arctic*, 34: 307–313.
- PETERSEN G.H. and CURTIS M.A. 1980. Differences in energy flow through major components of subarctic, temperate and tropical marine shelf ecosystems. — *DANA*, 1: 53–125.
- SAKSHAUG E. (ed) 1992. *Okosystem Barentshavet*. PRO MARE, Trondheim, 304 pp.
- SAKSHAUG E. 1997. Biomass and productivity distributions and their variability in the Barents Sea. — *ICES Journal of Mar. Sci.*, 54: 341–350.
- SCHNEIDER D.C., HUNT G.L. and HARRISON N.M. 1986. Mass and energy transfer to seabirds in the southeastern Bering Sea. — *Continental Shelf Res.*, 5: 241–257.
- STEMPNIEWICZ L. 1980. Factors influencing the growth of little auk (*Plautus alle* L.) nestlings on Spitsbergen. — *Ekol. Pol.*, 28: 557–581.
- STEMPNIEWICZ L. and JEZERSKI J. 1987. Incubations shifts and chick feeding rate in the little auks (*Alle alle*) in Svalbard. — *Ornis Scandinavia*, 18: 289–305.
- STEMPNIEWICZ L. and WĘŚLAWSKI J.M. 1992. Outline of trophic relationships in Hornsundfjord, SW Spitsbergen. — *In*: K.W. Opaliński and R.Z. Klekowski (eds), *Landscape, Life World and Man in High Arctic*. Institute of Ekology PAS; 271–298.
- SZANIAWSKA A. and WOŁOWICZ M. 1986. Changes in the energy content of common species from Hornsund, SW Spitsbergen. — *Polar Res.*, 4: 85–90.
- TANTSIURA A.I. 1959. O techniakh Barentseva morja. — *Trudy PINRO*, 11: 35–53.
- TASKER M.L., JONES P.H., DIXON T.J. and BLAKE B.F. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. — *Auk*, 101: 567–577.

- WELCH H.E., BERGMANN M.A., SIEFERD T.D., MARTIN K.A., CURTIS M.F., CRAWFORD R.E., CONOVER R.I. and HOPE H. 1992. Energy flow through the marine ecosystem of the Lancaster Sound region, Arctic Canada. — *Arctic*, 45: 343–357.
- WĘSŁAWSKI J.M., JANKOWSKI A., KWAŚNIEWSKI S., SWERPEL S. and RYG M. 1991. Summer hydrology and zooplankton in two Spitsbergen fjords. — *Pol. Polar Res.*, 12: 445–460.
- WĘSŁAWSKI J.M. and KWAŚNIEWSKI S. 1990. The consequences of climatic fluctuations for the food web in Svalbard coastal waters. — *In: M. Barnes and R.N. Gibson (eds), Proc. 24th Europ. Mar. Biol. Symp.*, Aberdeen Univ. Press; 281–295.
- WĘSŁAWSKI J.M., STEMPNIEWICZ L. and GALAKTIONOV K.M. 1994. The food and feeding of little auk from Franz Josef Land. — *Polar Res.*, 13: 173–181.
- WĘSŁAWSKI J.M., STEMPNIEWICZ L., MEHLUM F. and KWAŚNIEWSKI S. 1999. Summer feeding strategy of the little auk (*Alle alle*) from Bjornoya, Barents Sea. — *Polar Biol.*, 21: 129–134.
- WILLIAMS R. and ROBINS D. 1980. Calorific, ash, carbon and nitrogen content in relation to length and dry weight of *Parathemisto gaudichaudi* (Amphipoda: Hyperidea) in the North East Atlantic Ocean. — *Mar. Biol.*; 247–252.
- WOŁOWICZ M. and SZANIAWSKA A. 1986. Calorific value, lipid and radioactivity of common species from Hornsund, SW Spitsbergen. — *Polar Res.*, 4: 79–84.

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## Streszczenie

Praca przedstawia wyniki zebrane w czasie siedmiu rejsów t/v *Oceania* na Morze Grenlandzkie, Norweskie i Barentsa, w sezonach letnich 1989–1995. Alczyk (*Alle alle*) był jednym z najliczniej obserwowanych ptaków morskich w rejonie badań. Biomasa makroplanktonu, który jest głównym pokarmem alczyka wahała się od 0.1 do ponad 1g mokrej masy w m<sup>3</sup> powierzchniowej warstwy wód (0–20 m głębokości). Alczyki występowały w zagęszczeniach do ponad 4000 ptaków na km<sup>2</sup>. Plankton wód atlantyckich (Morze Norweskie) miał wysoką biomasa w 1 m<sup>3</sup>, ale zdominowany był przez małe organizmy (głównie copepoditowe stadia *Calanus finmarchicus*). Plankton przybrzeżnych wód fjordowych składał się również głównie z małych (poniżej 3 mm) organizmów× (głównie *Pseudocalanus* spp). Natomiast arktyczny plankton Morza Barentsa miał niską biomasa, lecz znaczny udział dużych organizmów (*Calanus glacialis*). Szacujemy, że 25% biomasy letniego zooplanktonu jest konsumowane przez ptaki, w najbardziej odwiedzanych rejonach żerowisk (stanowi to około 8% produkcji zooplanktonu). Średnio, w badanym obszarze alczyk konsumuje około 1% biomasy zooplanktonu.