Polar Biol (1992) 12: 685-692

Polar Biology

Summer diet of seabirds feeding in sea-ice-covered waters near Svalbard

O.J. Lønne[1] **and G.W. Gabrielsen**[2]

[1] The Norwegian College of Fishery Science, University of Tromsø, N-90037 Tromsø, Norway
[2] The Norwegian Institute for Nature Research, c/o Tromsø Museum, University of Tromsø, N-9006 Tromsø, Norway

Received 10 January 1992; accepted 16 May 1992

Summary. We describe the summer diets of four seabird species, Kittiwake (*Rissa tridactyla*), Little Auk (*Alle alle*), Black Guillemot (*Cepphus grylle*) and Brünnich's Guillemot (*Uria lomvia*) collected in sea-ice-covered waters near Svalbard. Birds collected in an area filled with young sea-ice, within the seasonal sea-ice zone, were compared with birds collected from the perennial sea-ice zone dominated by multiyear ice. Pelagic Crustacea and fish dominated the diet of birds feeding in young ice, while sympagic Crustacea and fish were most important in the diet of birds feeding in multiyear ice. *Boreogadus saida* was the most important fish food item. *B. Saida* was present in the ice in both areas, while sympagic Crustacea were lacking in the area filled with young ice. Important food items in young ice were *B. saida* (Black Guillemots and Kittiwakes), *Calanus* sp. (Little Auks) and *Pandalus borealis* (Brünnich's Guillemot). *B. saida* (Black Guillemots, Kittiwakes, Brünnich's Guillemots), *Gammarus wilkitzkii* (Brünnich's Guillemot, Black Guillemot) and *Apherusa glacialis* (Little Auk) were most important in multiyear ice. In general, Black Guillemots and Kittiwakes fed on fish, whereas Brünnich's Guillemots fed on the larger, and Little Auks on the smaller, Crustacea. The importance of sympagic species in the diet of seabirds is thought to be closely related to the age and history of the ice in the feeding area.

Introduction

The Barents Sea and the waters surrounding Svalbard support some of the largest concentrations of seabirds in the world (Belopol'skii 1957; Zenkevitch 1963; Norderhaug et al. 1977). These birds constitute a component of the arctic marine ecosystem and they form an important linkage between the marine and terrestrial ecosystems by the transport of nitrogen-rich guano and nutrients from the sea to the land (Gabrielsen and Mehlum 1989).

Correspondence to: O.J. Lønne

The Kittiwake (*Rissa tridactyla*) is the most numerous species of Laridae in the Svalbard area and the Little Auk (*Alle alle*) the smallest and the most abundant alcid species. Whereas Brünnich's Guillemot (*Uria lomvia*) have the highest biomass, the Black Guillemot (*Cepphus grylle*) have the lowest in the same area (Gabrielsen and Ryg 1992). The four seabird species included in this study belong to two main ecological groups. Kittiwakes are surface feeders and restricted to the upper 0.5–1 m of the water column (e.g Belopol'skii 1957; Ashmole 1971), while Little Auks, Brünnich's Guillemots and Black Guillemots are all divers and may locate their prey in the open water masses, near the bottom or at the ice-water interface.

The sympagic fauna (i.e. sea-ice fauna), including the polar cod (*Boreogadus saida*), represents a possible food source for diving seabirds. Sympagic fauna is generally more abundant within the perennial sea-ice zone than in the seasonal sea-ice zone. Most data on seabird diets in ice are from fast-ice or pack-ice within the seasonal sea-ice zone (e.g. Bradstreet 1980; Mehlum and Gjertz 1984; Cairns 1986). Less information is available from areas in the perennial sea-ice zone. The aim of this study is to describe and compare the diets of birds feeding in areas with a seasonal sea-ice cover with the diets of birds from areas with a perennial sea-ice cover. Moreover, emphasis has been put on comparing bird diets with the composition of the sympagic fauna collected from the same locations.

Material and methods

A total of 175 seabirds of four species were collected during two cruises; in the western Barents Sea in April–May 1985 and in the western Barents Sea and north of Svalbard in July-August 1986 (Table 1). Actively feeding birds were shot from the ice or from rubber boats.

Stations visited during the 1985 cruise and stations 2 and 3 visited in 1986 (Table 1) were between 76°23'N–77°41'N and 18°11'E–25°39'E in the western Barents Sea. Typical for this area is a seasonal covering of first-year ice. In 1985, the ice was estimated to be 1–3 months old. In 1986, the same area was partly filled with multiyear ice floes at the time of sampling. The remaining locations visited during the 1986 cruise were between 80°00′N–81°39′N and 02°03′E–31°51′E in the perennial sea-ice zone north of Svalbard. Multiyear ice dominated at these stations. To compare the diets at the two different ice-type locations the 1985 data is pooled and referred to as FYI (i.e. first-year ice) samples and the 1986 data is referred to as MYI (i.e. multiyear ice) samples.

The stomach and oesophagus were dissected out from each bird and preserved in 80% ethanol shortly after collection. Stomach contents were later sieved through a 0.5 mm sieve. Food items were identified to species level or lowest possible taxa. Dry weights of the food items were obtained by drying at 60°C until constant weight was reached. In cases where we were unable to separate different prey species, their occurrence was noted and their summed dry weight assigned to the nearest higher taxon. The results of stomach analysis are presented in terms of two variables:

1. The number of stomachs containing one or more individuals of each food category was recorded, and its frequency of occurrence (F%) calculated among the non-empty stomachs (Hyslop 1980).
2. The total dry weight of each food category from all stomachs was expressed as a percentage of total dry weight of the pooled stomach contents, giving an indication of the relative importance (I%) of each food category (Eliassen and Jobling 1985).

Occurrence of otoliths was treated separately, because their residence time in the stomach is believed to deviate from that of soft parts (Jobling and Breiby 1986). Otoliths were identified to the species level when possible. Length (l) and width (w) of *B. saida* otoliths were measured to nearest 0.05 mm using a binocular microscope. The linear relation (in mm) between l and w was estimated by the method of least squares among all available l, w pairs:

$$l = -1.92 + 2.627\ w\ (r^2 = 0.92)$$

This relation was used to estimate l in cases where w was the only parameter possible to measure. The length was measured for all otoliths in the FYI samples, but had to be estimated for 107 otoliths in the MYI samples. Total lengths of ingested *B. saida* were estimated using the relationship between otolith length and total length derived from *B. saida* caught in the ice (Lønne and Gulliksen 1989). The linear relation (in mm) between the length of otoliths and total length of all fish sampled ($n = 97$) was calculated using the method of least squares:

$$\text{Total length} = 16.4 + 21.8\ \text{otolith length}\ (r^2 = 0.94)$$

No attempt was made to calculate dry weight or relative importance (I%) of Polychaeta because jaws were usually the only remains.

To compare the availability of sympagic fauna (including *B. saida*) with the diet of the four seabird species, feeding locations were searched and sampled using SCUBA-equipment. Occurrence and density of the invertebrate sympagic fauna (Lønne and Gulliksen 1991a, b) and size and diet of *B. saida* (Lønne and Gulliksen 1989) were treated separately.

To study the pattern of feeding behaviour among the bird species sampled, multivariate methods recommended for use in benthic ecology (Field et al. 1982) were applied to the data set. A matrix was constructed in which 9 groups were described by the relative frequency of occurrence of 14 taxa of prey species. One group consisted of the pooled data from one bird species sampled in one of the two ice categories. Sympagic species from the same locations as birds were shot in MYI were also pooled to make one group. No sympagic fauna was found in FYI (Lønne and Gulliksen 1991a). The Bray-Curtis index (Bray and Curtis 1957) was adopted as a measure of dissimilarity. A dendrogram divided the groups, by group-average sorting, at an arbitrary similarity level of 50%. Multi-dimensional scaling (MDS) (Kruskal and Wish 1978) was also applied, based on the Bray-Curtis dissimilarity matrix, and was thus directly comparable to the dendrogram.

Results

Diet

Four invertebrate species (Crustacea) were recorded and identified from stomach contents of the seabirds collected from FYI (Tables 2, 3). 34% of the collected birds had empty stomachs (Table 1). Bones and soft parts from fish were recorded in three of the species (Tables 2, 3). 57% of the identified otoliths were from *B. saida*, suggesting that *B. saida* was the most frequently occurring fish food item. The median length of these otoliths was 2.90 mm, corresponding to a fish length of 7.9 cm (Fig. 1). Otoliths from six fish species (*B. saida*, *Lycodes* sp., *pollachius virens*, *Mallotus villosus*, *Gadus morhua*, *Melanogrammus aeglefinus*) were recorded (Table 4).

Table 1. Sampling stations, dates, localities and number (no.) of seabirds collected. () = number of birds with empty stomachs. BrGu = Brünnich's Guillemot, LiAu = Little Auk, BlGu = Black Guillemot, Kw = Kittiwake

St. no	Date	Locality		BrGu no.()	LiAu no.()	BlGu no.()	Kw no.()
1985							
1	28. Apr	76°23′N	18°11′E	2(1)		1(0)	8(1)
2	30. Apr	76°48′N	23°13′E				10(8)
3	3. Mai	76°54′N	25°39′E	23(6)			
4	8. Mai	77°30′N	18°50′E		10(3)	1(0)	1(0)
Total				25(7)	10(3)	2(0)	19(9)
1986							
2	24. Jul	77°15′N	23°00′E	7(2)	1(0)		5(2)
3	25. Jul	77°41′N	19°06′E	1(0)	17(1)		6(1)
5	27. Jul	80°00′N	18°07′E	2(0)	10(0)	8(0)	
7	30. Jul	81°04′N	23°50′E		9(1)	2(0)	9(0)
11	2. Aug	80°17′N	31°51′E		3(0)	1(0)	5(1)
13	3. Aug	80°01′N	18°03′E	8(0)			1(1)
17	5. Aug	81°39′N	14°00′E				1(0)
19	6. Aug	80°06′N	02°03′E		21(8)		2(0)
Total				18(2)	61(10)	11(0)	29(5)

Table 2. Frequency of occurrence (F%) of prey items among non-empty stomachs of seabirds sampled in first-year ice (FYI) and multiyear ice (MYI). *indicates sympagic species. Bird species codes see Table 1. n = number of birds with stomach content. F% is defined in the text.

Bird species	BrGu		LiAu		BlGu		Kw	
Ice category	FYI	MYI	FYI	MYI	FYI	MYI	FYI	MYI
Sample size (n)	18	16	7	51	2	11	10	24
Prey items:								
Indet.	27.8	18.8						
Polychaeta								
Nereis sp.								16.7
Crustacea								
Crustacea ind.		6.3		23.5				4.2
Copepoda								
Calanus sp.			100.0	33.3				
Mysidacea								
Mysis oculata		6.3				8.3		
Amphipoda								
Amphipoda ind.	44.4	37.5		60.8				
Parathemisto libellula	16.7	18.8		23.5				16.7
**Apherusa glacialis*				37.3				4.2
**Onisimus* sp.		6.3		13.7				
**Gammarus wilkitzkii*		50.0		17.6		33.3		
**Gammaracanthus-loricatus*		6.3						
Anonyx sp.	5.6							
Euphausiacea								
Thysanoessa inermis		12.5						
Malacostraca								
Pandalus borealis	61.1							
Pisces								
Bones and soft parts	11.1	37.5			100.0	91.7	100.0	100.0
Chaetognatha								
Sagitta sp.			100.0					
Mammals								
blubber							10.0	

Nine species of Polychaeta or Crustacea were recorded in the stomachs of the birds from MYI (Tables 2, 3). Crustacea were by far the most frequent component. Remains of Polychaeta were only recorded in Kittiwakes. 14% of the examined stomachs were empty (Table 1). Soft parts of fish were found in all species except for the Little Auk. 86% of the identified otoliths were from *B. saida*, indicating that *B. saida* was the most frequently occurring fish food item (Table 4). The median length of these otoliths was 4.95 mm, corresponding to a fish length of 12.4 cm (Fig. 1). The median length of otoliths from the MYI samples was significantly larger than that of otoliths from the FYI samples (95% conf. int., see Fig. 1). Since FYI samples were taken in April–May and MYI samples in July–August this difference might be due to growth during the summer season. The mean annual length increase of 2.5 cm from one- to two-year old fish, from Lønne and Gulliksen's data (Lønne and Gulliksen 1989), was therefore added to the FYI data to account for growth. FYI and MYI sample medians were, however, still significantly different (Fig. 1). Otoliths from four different fish species (*B. saida*, *Myoxocephalus scorpius*, *Gymnocanthus tricuspis*, *Benthosema glaciale*) were found (Table 4) in this group of birds.

Pandalus borealis dominated the diet of Brünnich's Guillemots collected from FYI, occurring in 61% of the non-empty stomachs and accounting for 66% of total stomach dry weight. The only other identifiable invertebrate species of importance was *Parathemisto libellula* (Tables 2, 3). Fish soft parts were recorded in two stomachs. Their relative importance as dry weight is embedded in the indeterminate group; they were inseparable from other material (Table 3). Otoliths from *B. saida*, *P. virens* and *Lycodes* sp. were recorded (Table 4), of which 90% were from *B. saida*.

Stomachs from Brünnich's Guillemot sampled in MYI (Table 1) contained Crustacea (Mysidacea, Amphipoda and Euphausicea) and fish (Table 2). Most frequently occurring in the diet was the sympagic amphipod *Gammarus wilkitzkii* (50%) and soft parts of fish (38%) (Table 2). The main contributors to the total stomach dry weight were fish (48%), *G. wilkitzkii* (16%) and the pelagic amphipod *P. libellula* (10%). Otoliths belonging to either *B. saida* or *M. scorpius* were found in 8 of the 18 stomachs (Table 4), 91% of the identifiable otoliths being from *B. saida*.

The copepod *Calanus* sp. and the chaetognath *Sagitta* sp. were recorded in all non-empty stomachs of Little Auks collected from FYI (Table 2). *Sagitta* sp. was represented as jaws only. All dry weights are related to *Calanus* sp. (Table 3); 30% of the examined stomachs were empty (Table 1).

Table 3. Relative importance of prey (I%) items in stomachs of seabirds sampled in first-year ice (FYI) and multiyear ice (MYI). * indicates sympagic species. Species codes see Table 1. I% is defined in the text.

Bird species	BrGu		LiAu		BlGu		Kw	
Ice category	FYI	MYI	FYI	MYI	FYI	MYI	FYI	MYI
Indet.	21.9	9.3						
Polychaeta								
Nereis sp.								
Crustacea								
Crustacea ind.		4.2		20.2				
Copepoda								
Calanus sp.			100.0	11.9				
Mysidacea								
Mysis oculata		5.1				2.7		
Amphipoda								
Amphipoda ind.	9.8	7.1		29.5				
Parathemisto libellula	2.6	10.2		3.5				2.1
**Apherusa glacialis*				30.0				
**Onisimus* sp.				1.2				
**Gammarus willkitzkii*		15.7		3.6		13.8		
**Gammaracanthus loricatus*		0.4						
Anonyx sp.								
Euphausiacea								
Thysanoessainermis		0.3						
Malacostraca								
Pandalus borealis	65.7							
Pisces								
Bones and soft parts		47.7			100.0	83.5	37.1	97.8
Chaetognatha								
Sagitta sp.								
Mammals								
blubber							62.9	

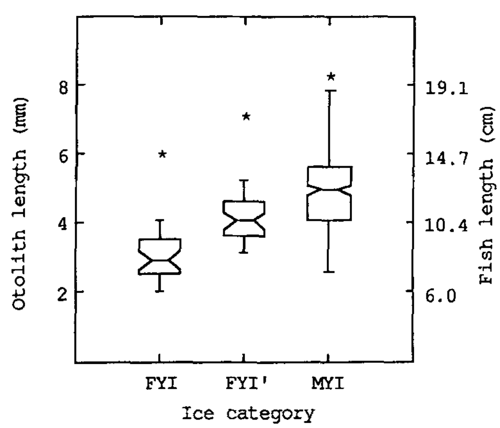

Fig. 1. Notched box plot (McGill et al. 1978) showing median lengths (1) of *B. saida* otoliths found in stomachs of birds sampled in first-year ice (FYI) and multiyear ice (MYI). FYI' is the FYI samples adjusted for growth (see text). Central horizontal line of the box indicates the median value. The edges of the box splits the upper and lower half of the ordered batch of numbers in two. The boxes are notched at the median and return to total width at the upper and lower 95% confidence interval values. *Whiskers* indicate the most extreme values still inside inner fences. * Values outside inner fences

In MYI samples, the diet of Little Auks again consisted only of Crustacea. Most frequent among the identified species was the sympagic amphipod *Apherusa glacialis* (37%) (Table 2), which also contributed most to the pooled stomach dry weight (30%, Table 3). Calanoid copepods occurred in 33% of the stomachs, accounting for 12% of the total dry weight. *P. libellula*, *Onisimus* sp. and *G. wilkitzkii* also occurred frequently; 16% of the Little Auk stomachs were empty (Table 1).

Two Black Guillemots were sampled from FYI, and both fed exclusively on fish (Table 2). *B. saida* otoliths occurred in both and *P. virens* in one (Table 4).

From MYI, 11 Black Guillemots were sampled. All stomachs contained organic material (Table 1). Fish soft parts accounted for 84% of the dry weight (Table 3) and were also the most frequently occurring food item (92%) (Table 2). All identifiable otoliths were from *B. saida*. The sympagic amphipod *G. wilkitzkii* occurred in 33% of the stomachs, accounting for 14% of the dry weight.

All Kittiwakes sampled from FYI fed on fish, but its relative importance (I%) was reduced to 37% due to the ingestion of one large portion of mammal blubber in one bird (Table 3). Six different species of fish were identified from otoliths, with *B. saida* and *P. virens* predominating (Table 4).

Kittiwake stomachs sampled from MYI (Table 1) contained Polychaeta, Crustacea (Amphipoda) and fish soft parts (Table 2). Fish soft parts accounted for 98% of the pooled stomach dry weights. Polychaetes occurred mostly as jaws and were identified as belonging to the heteronereis group, and a few specimens were complete enough to be identified as *Nereis pelagica*. Identifiable

Table 4. Number of birds with otoliths and total number of otoliths found (no.) in seabirds sampled in first-year ice (FYI) and multiyear ice (MYI). Bird species codes see Table 1

Bird species	BrGu		BlGu		Kw	
Ice category	FYI	MYI	FYI	MYI	FYI	MYI
Number of birds with otoliths	3	8	2	10	14	26
	no.	no.	no.	no.	no.	no.
Indet.	0	9	0	27	4	22
Boreogadus saida	17	41	6	65	11	186
Myoxocephalus scorpius		4				
Gymnacanthus tripcuspus						34
Benthosema glaciale						9
Pollachius virens	1		1		12	
Lycodes sp.	1				2	
Mallotus villosus					1	
Gadus morhua					7	
Melanogrammus aeglefinus					1	

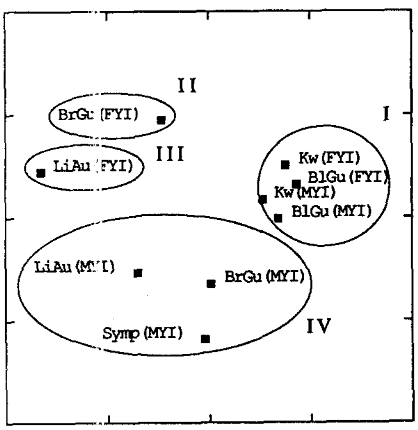

Fig. 2. Ordination of 9 groups of birds based on frequency of occurrence of food items in bird stomachs and of sympagic fauna in MYI. The groups were compared by using multidimensional scaling in 2-dimensions on the Bray-Curtis measure of similarity. Clusters *I – IV* were distinguished in a dendrogram, at a similarity level of 50% (not shown), and are superimposed here by encircling each cluster. Axis scales are purely arbitrary. *Symp* = sympagic fauna sampled in the ice. For the other group codes see abbreviations in Table 1. *FYI* = samples from first-year ice, *MYI* = samples from multiyear ice

amphipods were *A. glacialis*, and *P. libellula* (Table 2). Of the identifiable otoliths, 81% were from *B. saida*. Otoliths from *G. tripcuspus* and *B. glaciale* were also present (Table 4).

Diet selectivity and food availability

In this study, Black Guillemot and Kittiwake were generally fish feeders (cluster I in Fig. 2), whilst Brünnich's Guillemot and Little Auk fed mostly on Crustacea (cluster II, III, IV in Fig. 2). Sympagic invertebrate species played an important role in the diet in MYI samples, but not in FYI samples (Tables 2, 3 and Fig. 2). Searches were made for sympagic fauna at nine localities with FYI and at 25 localities with MYI, including the localities where seabirds were sampled. In FYI areas, only five large *G. wilkitzkii* were observed. Sympagic fauna was common at all localities with MYI (Lønne and Gulliksen 1991a,b).

Planktonic species were not systematically sampled during the cruises. Calanoid copepods and the amphipod *P. libellula*, however, were occasionally observed under the ice and sampled in the sympagic sampling gear in both ice categories (Lønne and Gulliksen 1991a,b).

B. saida was sampled from the ice in both FYI and MYI areas, but quantitative sampling was impossible due to its mobility and the difficulty of catching the fish in the ice (Lønne and Gulliksen 1989).

Discussion

Feeding methods

The Crustacea eaten by Kittiwakes in this study can be reached from the surface. *P. libellula* occurs occasionally in dense swarms both between and underneath ice floes (Gulliksen 1984; O.J. Lønne, personal observation). *A. glacialis* is normally associated with the lower surfaces of the sea-ice, but can be found in high densities on vertical walls of ice floes (Lønne and Gulliksen 1991b). *B. saida* is found both pelagically and near the bottom in areas without ice cover (Falk-Petersen et. al. 1986). In the ice, *B. saida* is mainly found in small schools between sandwiched ice floes or in holes and cracks in the ice (Lønne and Gulliksen 1989). We have also observed *B. saida* swimming near the surface between ice floes where it can be reached by Kittiwakes. Another possible food source for Kittiwakes was the fish which were exposed as the ship turned over ice floes. Kittiwakes feeding on *B. saida* thrown onto the ice or swimming among floes behind the boat have been observed on a number of occasions (O.J. Lønne, personal observation).

For the Little Auks, Brünnich's Guillemots and Black Guillemots, the water column and the ice-water interface were the only feeding grounds of importance in this study. The Crustacea eaten were either pelagic or sympagic. One possible exception was the lyssianasid amphipod *Anonyx* sp. *Anonyx nugax* has, however, been found associated with ice in the same area (Lønne and Gulliksen 1991a). *G.*

wilkitzkii and *Onisimus* sp. are found in cracks and small holes on the lower surface of sea-ice (Lønne and Gulliksen 1991a). To feed on these organisms, the birds will have to dive underneath the floes and pick them out of their hiding places. The only indications of feeding near the bottom were four otoliths from *M. scorpius* found in Brünnich's Guillemots from MYI.

Feeding in first-year ice versus multiyear ice

The three diving seabird species included in this study fed at the sea-ice interface. The sympagic faunal assemblage can be divided into three groups; the autochthonous sympagic species (i.e. permanent residents of the ice), the pelago-sympagic species (i.e. sympagic species associated with the water column when not found in the ice) and the bentho-sympagic species (i.e. sympagic species associated with the benthos when not found in the ice) (Gulliksen and Lønne 1991), of which the two first are of importance in the areas covered by this study.

A. glacialis. Onisimus sp. and *G. wilkitzkii* are autochthonous sympagic species. Their main distributional area is within the perennial sea-ice zone of the Arctic Ocean. They are believed to colonize new ice by moving along the lower ice surface. Colonization of new ice in the Barents Sea is therefore believed to take place from old floes drifting in from the perennial sea-ice zone further north. The density of autochthonous sympagic fauna in the Barents Sea is closely related to the amount of ice transported into the area. Densities in the western Barents Sea vary normally between 0 and 0.1 $g\,m^{-2}$ (wet weight) (Gulliksen 1984; Lønne and Gulliksen 1991a), while densities inside the perennial sea-ice zone are generally higher (1–10 $g\,m^{-2}$) (Barnard 1959; Mel'nikov and Kulikov 1980; Lønne and Gulliksen 1991b).

The lack of autochthonous sympagic fauna in the spring of 1985 was associated with persistent southerly winds during the winter, that pushed ice from the Barents Sea northwards into the Arctic Basin increasing the distance between the studied area and the first-year/multiyear ice boundary. The reverse was true in late summer of 1986. Multiyear ice had drifted south and replaced the young ice formed in the Barents Sea, resulting in biomass values of sympagic fauna of about 2 $g\,m^{-2}$. North of Svalbard, the average biomass values were in the order of 5 $g\,m^{-2}$ (Lønne and Gulliksen 1991b).

B. saida is the only pelago-sympagic species recorded in the study area. The colonization of the ice habitat by pelago-sympagic species is related to their presence in the underlying water masses and not to the distribution of old and new ice. *B. saida* eaten by the birds may have been associated with the open water masses, but there is some evidence that the birds collected in this study had been feeding upon *B. saida* associated with the ice. Falk-Petersen et al. (1986) found a length distribution of 1.5–18 cm of *B. saida* collected during pelagic trawl surveys around Svalbard, and that *B. saida* caught in the upper 15–80 m were 0-group fish (length range 1.5 to 7cm). Fish collected in the ice, however, were either one or two years old and had a length range of 6–17 cm (Lønne and Gulliksen 1989). The estimated length of fish eaten by birds in this study was 6–19.7 cm. Lønne and Gulliksen (1989) found that one-year-old fish dominated the populations of *B. saida* collected in first year ice, as opposed to more evenly mixed populations of one- and two-year-old fish in multiyear ice. They suggest that this difference is controlled by the seasonality in the ice covering. Melting of the ice forces the fish into open water, while in old ice the fish stay until maturity and descend to greater depths during spawning. This agrees well with the findings in this study where the median length of *B. saida* otoliths from MYI samples were significantly higher than the ones from FYI. Together, this suggests that the fish-feeders foraged at the sea-ice interface and that the sea-ice interface is of importance as a feeding ground, even in years when the autochthonous sympagic fauna is lacking or present in low numbers.

In our study, the proportion of empty stomachs was 25% in FYI and 14% in MYI samples. The number of different invertebrate food species was four in FYI and nine in MYI. The proportion of *B. saida* otoliths in the stomachs was only 57% in FYI in contrast to 86% in MYI. This supports the idea that sympagic species are an important food source for diving sea-birds which feed in ice-covered waters. However, the FYI samples were taken in the spring, and the MYI samples in the late summer, and partly in two different areas. Differences in the composition and density of the planktonic community may have influenced their choice. Bradstreet (1982) argued that amphipods (*Parathemisto* spp. and *A. glacialis*) were preferred food items for Little Auks compared to Calanoid copepods due to greater caloric intake per item.

Dietary differences

The main dietary difference between the four species was the large amount of fish (mainly *B. saida*) eaten by Kittiwakes and Black Guillemots (and partly Brünnich's Guillemots in MYI), in contrast to the dominance of Crustacea found in Little Auks and Brünnich's Guillemots. The presence of fish-feeders from FYI and MYI samples within the same cluster in Fig. 2 is consistent with our observations that *B. saida* was present in both FYI and MYI.

Brünnich's Guillemots and Little Auks fed on pelagic Crustacea in FYI and on autochthonous sympagic Crustacea in MYI, which has placed them in cluster II, III and IV respectively (Fig. 2). This is consistent with the fact that autochthonous sympagic species were absent from the FYI at the time of sampling in 1985 and present in high densities in the MYI sampled in 1986. In FYI areas, Little Auks fed exclusively on calanoid copepods while Brünnich's Guillemots preferred *P. borealis* and *P. libellula*. This has led to the separation of the two species into separate clusters (II, III in Fig. 2). In MYI areas, Little Auks fed on the sympagic fauna and on *A. glacialis* in particular, whilst Brünnich's Guillemots selected *B. saida* and *G. wilkitzkii*. They fed in the same habitat in both sampling periods, but with a tendency for Little Auks to select the smaller species and Brünnich's Guillemot the larger.

The differences in diet of the birds between the two ice categories reflects the availability of food and indicates an opportunistic feeding behaviour typical of species inhabiting this environment.

Comparison with other studies

In a summer study in the northern Barents Sea (Mehlum and Gjertz 1984), birds were collected in ice-covered waters. *B. saida* dominated the Kittiwake diet, whilst Black Guillemot fed mainly on *B. saida* and *G. wilkitzkii*. The average length of fish ingested was estimated to be 13 cm for both Kittiwakes and Black Guillemots. The Little Auks fed upon *Calanus finmarchicus*, *P. libellula* and *A. glacialis*. The only Brünnich's Guillemot collected contained *P. libellula*. Sympagic fauna was studied at the same locations (Gulliksen 1984). *A. glacialis* and *G. wilkitzkii* were generally the most conspicuous organisms in the ice and biomass values at individual stations varied form less than 0.01–1.15 g m^2, including calanoid copepods and *P. libellula*. Another study was conducted in the marginal ice zone in the Barents Sea in summer 1984 (Gjertz et al. 1985). The two Black Guillemots collected contained *B. saida* and *G. wilkitzkii*. Three Brünnich's Guillemot contained *P. libellula*. *B. saida* dominated the diet of the 18 Kittiwakes collected. Estimated mean length of *B. saida* eaten by Kittiwakes was 10.6 cm and by Black Guillemots 9.7cm. These estimated fish lengths are similar to those of our study and those of fish caught in the ice by Lønne and Gulliksen (1989). In the autumn in Hornsund, western Spitsbergen, *B. saida* and *P. libellula* were the most important food items in the four seabird species included in our study (Lydersen et al. 1989). Mean length of *B. saida* eaten by the seabirds was less than 5 cm for all four species. This corresponds to the O-group found in the upper 80 m in trawl surveys by Falk-Petersen et al. (1986). The diet of the three diving species Brünnich's Guillemot, Black Guillemot and Little Auk consisted of both pelagic and benthic species.

In the seasonally ice-covered Barrow Strait area, Canada, Bradstreet (1980) compared the spring diet of Brünnich's Guillemots and Black Guillemots collected along a coastal ice edge and at the edges of landfast ice further offshore. At coastal ice edges, Brünnich's Guillemot diet was dominated by *B. saida* (74%, biomass) and *Onisimus littoralis* (18%). Black Guillemot diet was dominated by *B. saida* (99%). At offshore edges, Brünnich's Guillemot took *B. saida* (96%), *Parathemisto* spp. (2%), and *O. glacialis* (2%). Black Guillemot caught *B. saida* (54%) and *O. glacialis* (35%). *A. glacialis* was also of some importance for both species at offshore ice edges. *O. littoralis* is a benthic amphipod that is found seasonally in high densities on the undersurface of ice above shallow water (e.g. Carey 1982). Cross (1982) studied the sympagic fauna of the fast-ice in Pond Inlet near Barrow strait in the spring 1979. He found the sympagic invertebrate macrofauna to be dominated by *A. glacialis*, *Ischyrocerus anguipes* and *O. glacialis*. The overall mean biomass of sympagic invertebrates in the study was 0.13 g m^{-2}. In another study in western Lancaster Sound and Baffin Bay, Canada, Bradstreet (1982) found a switch in the diet of Little Auks from spring to late summer. In May and June, Little Auks ate mostly copepods (99–100%). In August, amphipods including *Parathemisto* sp., *A. glacialis* and *Onisimus glacialis* became more important. He concluded that *O. glacialis* and *A. glacialis* were closely associated with the undersurface of ice pans that drifted through the study area.

In this study, we have given some evidence that *B. saida*, living in ice, were important in the diet of seabirds in both young and old ice areas. The autochthonous sympagic species were important in the diet of birds feeding in the perennial sea-ice zone north of Svalbard. Sympagic fauna have previously been reported to be a part of their diet in Arctic ice-filled waters (e.g. Bradstreet 1982; Mehlum and Gjertz 1984; Gjertz et al. 1985), but not to such an extent as in this study. Biomass values of the sympagic fauna from the area north of Svalbard was estimated to be in the order of 5 g m^{-2} (Lønne and Gulliksen 1991b). Lønne and Gulliksen (1991b) have estimated that in the order of 7.10^5 tons (wet weight) of sympagic fauna are transported with the ice in the transpolar drift stream through this area and into the Farm Strait every year. Biomass values of the sympagic fauna in the Barents Sea are typically in the order of 0.1g m^{-2} and vary annually with the age and history of its ice substrate (Gulliksen 1984; Lønne and Gulliksen 1991a). It is therefore suggested that the importance of the sympagic fauna as food for seabirds becomes more important and more reliable as one moves north from the seasonally ice-covered Barents Sea and into the permanently ice-covered areas north of Svalbard.

Acknowledgements. This publication is a contribution from the Norwegian Research Programme for Arctic Ecology (Pro Mare) and has been financed by the University of Tromsø and the Norwegian Research Council for Science and Humanities (NAVF). The authors would like to thank Ø. Kaasa for help during the analysis of the food samples, and B. Seim and H. Dahlen for help with the collection of the birds. We thank R. Barrett, C. Lydersen, B. Gulliksen and J.O. Bustnes and the reviewers E. Sakshaug and J. Piatt for valuable comments on the manuscript.

References

Ashmole NP (1971) Sea-bird ecology and the marine envirnoment. Avian Biol 1:223–286

Barnard JL (1959) Epipelagic and under-ice amphipoda (Crustacea) of the central Arctic Basin. Scientific studies at Fletcher's Ice Island T-3, 1952-1955. Geophys Res Papers 63:115–153

Belopol'skii LO (1957) Ecology of sea colony birds of the Barents Sea. Israel program for scientific translations (Jerusalem 1961), 346 pp

Bradstreet MSW (1980) Thick-billed murres and Black Guillemots in the Barrow Strait area, NWT, during spring: diets and food availability along ice edges. Can J Zool 58:2120–2140.

Bradstreet MSW (1982) pelagic feeding ecology of Dovekies, *Alle alle*, in Lancaster Sound and Western Baffin Bay. Arctic 35:126–140.

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27:325–349

Cairns DK (1986) Diet and foraging ecology of Black Guillemots in northeastern Hudson Bay. Can J Zool 65:1257–1263

Carey Jr AG (1982) Shallow southwest Beaufort Sea macrofauna: interactions with the epibenthic community. EOS 63:949

Cross WE (1982) Under-ice biota at the Pond Inlet ice edge and in adjacent fast ice areas during spring. Arctic 35:13–27

Eliassen J-E, Jobling M (1985) Food of the roughthead grenadier, *Macrourus berglax*, Lacepede in North Norwegian waters. J Fish Biol 26:367–376

Falk-Petersen I-B, Frivoll V, Gulliksen B, Haug T (1986) Occurrence and age/size relations of polar cod, *Boreogadus saida* (Lepechin), in Spitsbergen coastal waters. Sarsia 71:235–245

Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. Mar Ecol Prog Ser 8:37–52

Gabrielsen GW, Mehlum F (1989) Thermoregulation and energetics of arctic seabirds. In: Bech C, Reinertsen RE (eds) Physiology of cold adaptation in birds. Plenum Press, New York, pp 137–145

Gabrielsen GW, Ryg M (1992) Sjøfugl og pattedyr. In: Sakshaug E et al. (eds) Økosystem Barentshavet. NINA, Trondheim

Gjertz I, Mehlum F, Gabrielsen, GW (1985) Food sample analysis of seabirds collected during the 'Lance'-cruise in ice-filled waters in eastern Svalbard 1984. Norsk Polarinst Rapp Ser 23:17pp

Gulliksen B (1984) Under-ice fauna from Svalbard waters. Sarsia 69:17–23

Gulliksen B, Lønne, OJ (1991) Sea ice macrofauna in the Antarctic and the Arctic. J Mar syst 2:53–61

Hyslop EJ (1980) stomach content analysis – a review of methods and their application. J Fish Biol 17:411–429

Jobling M, Breiby A (1986) The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. Sarsia 71:265–274

Kruskal JB, Wish M (1978) Multidimensional scaling. Sage Publications, Beverly Hills, Calif, 93pp

Lydersen C, Gjertz I, Weslawski JM (1989) Stomach contents of autumn-feeding marine vertebrates from Hornsund, Svalbard. Polar Rec 25:107–114

Lønne OJ, Gulliksen B (1989) Size, age and diet of polar cod, *Boreogadus saida* (Lepechin 1773), in ice covered waters. Polar Biol 9:187–191

Lønne OJ, Gulliksen B (1991a) On the distribution of sympagic macro-fauna in the seasonally ice covered Barents Sea. Polar Biol 11:457–469

Lønne OJ, Gulliksen B (1991b) Sympagic macro-fauna from multiyear sea-ice near Svalbard. Polar Biol 11:471–477

McGill R, Tukey JW, Larsen WA (1978) Variations of box plots. Am Stat 32:12–16

Mel'nikov IA, Kulikov AS (1980) Cryopelagic fauna of the central Arctic Basin. In: Vinogradov M E, Mel'nikov I A, (eds) Biologiya tsentral'nogo arkticheskogo Bassejna. Can Trans Fish Aquat Sci 4910. Moskva, Nauka, pp 97–111

Mehlum F, Gjertz I (1984) Feeding ecology of seabirds in the Svalbard area – a preliminary report. Norsk Polarinst Rapp Ser16 41pp

Norderhaug M, Brun E, Møllen GU (1977) Barentshavets sjøfuglressurser. Medd Norsk Polarinst 104:1–119

Zenkevitch C (1963) Biology of the seas of the USSR. Allen & Unwin, London, 136 pp