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Bente Brekke · Geir Wing Gabrielsen

Assimilation efficiency of adult Kittiwakes and Brünnich's Guillemots fed Capelin and Arctic Cod

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Abstract The mean assimilation efficiencies of 10 adult Kittiwakes (*Rissa tridactyla*) and 10 Brünnich's Guillemots (*Uria lomvia*) fed on Capelin (*Mallotus villosus*) were 77.5% and 74.4%, respectively. When fed on Arctic Cod (*Boreogadus saida*) they were 83.1% and 78.2%, respectively. After correction for nitrogen retention, the assimilation efficiencies decreased to 72.2%, 70.6%, 81.2% and 74.7%, respectively. Kittiwakes and Brünnich's Guillemots seem to have the same ability to utilize the energy of the different food items. The differences in assimilation efficiencies when fed two fish species was mainly related to the fat content of the fish.

Introduction

The Barents Sea is very productive and supports one of the largest seabird populations in the world (Belopol'skii 1957; Løvenskiold 1964; Zenkevitch 1963). These seabirds constitute a major component of the marine ecosystem and form an important link between the terrestrial and the marine eco systems, especially on Svalbard, Frans Josef Land and Novaja Zemlja. Here they transport nitrogen-rich nutrients from the sea to the land (Gabrielsen and Mehlum 1989).

In order to determine the energy flow through seabird populations or communities, it is essential to know their feeding habits (Furness and Barrett 1985; Mehlum and Gabrielsen 1993), their energy and food requirements (Furness 1978; Croxall and Prince 1982; Furness and Barrett 1985; Bailey 1986; Cairns et al. 1991; Gabrielsen et al. 1987, 1991a; Gabrielsen 1994) and how efficient they are at utilizing different food items. It is thus important to determine their assimilation efficiency when they are eating some of the most important prey species in the area.

Previous studies of assimilation efficiencies in chicks and adult seabirds show inter specific variation (Dunn 1975; Cooper 1977; 1978, 1980; Copestake et al. 1983; Adams 1984; Heath and Randall 1985, Jackson 1985, 1990; Brugger 1993) and variation between prey types (Copestake et al. 1983, Jackson 1986). The assimilation efficiency varies between 54 and 90% (Cooper 1978; Dunn 1975) with an average of 75% (Furness 1978).

Seabirds feed on different prey species at different times of the year (Mehlum and Gabrielsen 1993). These prey species often vary considerably in energy-, lipid-, protein- and water content throughout the year (Jangaard 1974; Montevecchi and Piatt 1984; Gabrielsen et al. unpubl.). Since the assimilation efficiency varies with the composition of the food, it is important, when estimating the seabirds' impact on marine resources, to take the energy-, fat- and protein content of different food items into account. This has generally been given low priority in earlier work modelling seabird energetics and food requirements (Furness 1978; Croxall and Prince 1982; Furness and Barrett 1985). This study reports on the assimilation efficiency of Kittiwakes (*Rissa tridactyla*) and Brünnich's Guillemots (*Uria lomvia*) eating Capelin (*Mallotus villosus*) and Arctic Cod (*Boreogadus saida*).

B. Brekke[1] · G.W. Gabrielsen (✉)[2]
Norwegian Polar Institute, P.O. Box 5072 Majorstua, N-0301 Oslo, Norway

Present addresses:
[1] GRID-Arendal, P.O. Box 1602 Myrene, N-4801 Arendal, Norway
[2] Norwegian Institute for Nature Research, c/o Tromsø Museum, University of Tromsø, N-9006 Tromsø, Norway

Material and methods

Feeding experiments were conducted in June–July 1985 and 1986 at the Research Station of the Norwegian Polar Institute in Ny-Ålesund (79°N, 12'E), Svalbard.

Ten egg brooding birds of each species (Kittiwakes and Brünnich's Guillemots) of unknown sex and age were caught at the

Krykkje-fjellet colony, Kongsfjorden, Svalbard. The birds were transported to Ny-Ålesund (6 km) and kept in individual plastic-covered wire-mesh cages (50 × 50 × 60 cm). They were supplied with sea water *ad libitum*. The cages were placed outdoors and protected against rain by a transparent plastic sheet. The birds were thus exposed to normal ambient temperatures and light conditions (midnight sun) at Svalbard. The mean ambient day temperature during the experimental period in 1985 was 6.8°C (± 1.4°C, range 3.8°C–13.5°C) and in 1986 5.2°C (± 1.8°C, range 0.6°C–9.8°C). Since the lower critical temperatures of Kittiwakes and Brünnich's Guillemots are 4.5°C and 2.0°C, respectively (Gabrielsen et al. 1988), the feeding experiments were thus done within the birds thermoneutral zone most of the time.

Each bird was used in two trials. In the first trial they were fed Capelin and in the second they were fed Arctic Cod. The fish were ordered for this study, and time and place for the different Capelin and Arctic Cod catches used are presented in Table 3. Both food items were frozen immediately at − 10°C until thawed before each feeding. Capelin and Arctic Cod are natural prey of breeding Kittiwakes and Brünnich's Guillemots in the Barents Sea (Furness and Barrett 1985; Lønne and Gabrielsen 1992; Mehlum and Gabrielsen 1993), and the fish sizes fed correspond to the size of fish these birds eat in the wild (Furness and Barrett 1985; Mehlum and Gabrielsen 1993). The birds that did not eat voluntarily were given food by hand.

The birds were given a three day adaptation period before and between each trial. Both trials lasted five to six days. The feeding trials were carried out consecutively, with only one food type being used in each trial.

The birds were weighed every morning before feeding using a Metler PE 16 (± 0.1 g) balance. They were fed 2–4 times every day. The daily ration of food to each bird was determined on the basis that the bird either maintained a constant body mass or gained mass slightly. The amount of food (Capelin and Arctic Cod) given each day during the trials are presented in Table 1.

Since the birds excrete faeces and uric acid (collectively known as guano) through a common cloaca, these samples were collected and analysed together. The guano was collected every morning from plastic-covered trays placed under each cage. As much guano as possible was transferred to individual pre-weighed cups, using a rubber spatula, and dried to constant weight at 60–80°C. These dried guano samples were homogenised and analysed to determine 1) energy content, using a Gallenkamp Autobomb (Automatic Adiabatic Bomb Calorimeter), and 2) nitrogen and carbon content, using an Elemental Analyzer CHN mod. 1106 (Carlo Erba Strumentazione) connected to a LDC model 308 Computing Integrator.

Samples of the food were collected every day. There was little variation between samples from the same trial period so food samples from each trial were lumped. The resulting four samples were homogenised and analysed for 1) water content by weighing sub samples before and after freeze-drying (HETOSICC type CD 52), 2) energy content (described above), 3) nitrogen and carbon content (described above), and 4) fat content by using a modified Folch procedure (Holm et al. 1973). Protein content was calculated from the nitrogen content using the conversion factor 6.25 (FAO/WHO 1973).

Assimilated energy in birds can be expressed as ingested energy minus energy in guano (Harris 1966). Assimilation efficiency was calculated for each food type for individual birds per day as the percentage assimilated energy of ingested energy using the formula:

$$AE = (GE_{in} - GE_{out})/GE_{in} \times 100 \quad (1)$$

in which AE is assimilation efficiency, GE_{in} is gross energy intake (kJ) and GE_{out} is gross energy excreted (kJ).

Values of AE were corrected for nitrogen retention (NR) using the formula:

$$AEn = (GE_{in} - (GE_{out} + NR))/GE_{in} \times 100 \quad (2)$$

in which NR = (nitrogen intake (g) − nitrogen excreted (g)) × 36.5 kJ/g nitrogen, where 36.5 kJ/g nitrogen is the mean energy content per gram urine-nitrogen in birds (Titus et al. 1959).

Assimilation efficiency can be corrected for faeces-metabolic and urine-endogenous energy losses. These losses increase in relative size with decreasing meal-sizes, and are relatively smaller when meal-sizes are at or above maintenance level. Thus, assimilation efficiency values not corrected for these losses approach the corrected values as meal sizes increase (Miller and Reinecke 1984). These losses were thus assumed to be relatively small in this study, and were therefore ignored.

Two-tailed Mann–Whitney U-tests (non-parametric) were used to determine the significance of difference between means for the different test groups, assuming significant difference for $p \leqslant 0.05$.

The Spearman correlation analysis (non-parametric) was used to determine the significance of dependence between parameters within different test groups, assuming significant correlation for $p \leqslant 0.05$.

Means are reported ± standard deviation or standard error, and occasionally with range.

Results

Body mass

The mean body mass of Kittiwakes and Brünnich's Guillemots when captured in the colony were 366 g (± 35 g) and 967 g (± 54 g) respectively (Table 2). During the adaptation period before the Capelin trial (the first three days of captivity), Kittiwakes and Brünnich's Guillemots lost 14.7% (± 3.1%) and 12.1% (± 2.2%) of their body mass, respectively (Table 2). Throughout the Capelin trial period the mean daily mass changes were 0.0% (± 0.7%) and + 0.7% (± 0.4%), respectively. During the adaptation period before the Arctic Cod trial, all birds gained ca. 6% of their body mass (Table 2). Throughout the Arctic Cod trial period the mean daily mass changes were + 1.0% (± 0.6%) and + 0.6% (± 0.7%), respectively.

Table 1 Mean (± SE) daily intake of food and excretion of guano by Kittiwakes and Brünnich's Guillemots when fed Capelin and Arctic Cod

		Food intake (g)	Guano output (dry mass) (g)
Kittiwake:	Capelin	141.4 ± 19.5	14.0 ± 1.8
	Arctic Cod	106.4 ± 12.1	10.9 ± 1.6
B. Guillemot:	Capelin	278.9 ± 24.3	26.7 ± 2.6
	Arctic Cod	267.1 ± 35.7	25.1 ± 5.2

Table 2 Body mass (± SE) of birds before and during the feeding experiments

	In the colony (g)	Capelin trial (g)	Arctic Cod trial (g)
Kittiwake	366 ± 35	312 ± 28	347 ± 21
B. Guillemot	967 ± 54	864 ± 41	884 ± 63

Diet

The Capelin used in 1985 and in 1986 had the same water-, protein-, fat- and energy content (Table 3). Arctic Cod (from both years) had a higher lipid- and a lower water content, thus a higher energy content than the Capelin.

Food intake

In Kittiwakes the food intake was 33% higher when eating Capelin then when eating Arctic Cod (Table 1). This is much more than the 4% difference found in Brünnich's Guillemots. Although food intake was reduced from the preceding Capelin period, all birds gained body mass from the first day they were given Arctic Cod. The mean dry mass of guano excreted per day was highest in both species when fed Capelin (Table 1).

Guano

The energy and nitrogen content of guano from both species was relatively stable between years (Table 4). Nitrogen content varied between 20–22% and the energy content between 11–12%.

Assimilation efficiency

Correction of assimilation efficiencies for nitrogen retention reduced the assimilation efficiencies by 2–7%. Two-tailed Mann Whitney U-tests showed significant differences between all combinations of AEn's ($p \leqslant 0.011$) of the different bird/food groups (Table 4). Both Kittiwakes and Brünnich's Guillemots had higher AEn's when fed Arctic Cod than when fed Capelin. Daily AEn's varied within 2% throughout the experimental period. This is assumed to be within the natural variation.

Discussion

Food quality

Freezing and thawing may cause tissue damage in fish, which again may cause it to be digested differently than fresh fish (Jackson 1986). However, Svalbard is a remote area with an extreme climate and variable weather, which makes the possibilities for catching fresh fish of the species and size every day very difficult. Using fish from the same catch would secure homogeneity of the food items within one experimental period.

Correction for nitrogen retention

The importance of correcting for nitrogen retention has long been recognized among poultry scientists (Sibbald 1982). This practice enables direct comparison of assimilation efficiency values between birds with different nitrogen requirements. Nitrogen correction

Table 3 Length and weight of diet (± SD) and mean (± SE) nutrient composition (wet mass) of diet

	Length of food items (cm)	Weight of food items (g)	H_2O (%)	protein (%)	fat (%)	energy (kJ/g)	Time/place of catch
Kittiwake: Capelin	10.4 ± 0.7	3.7 ± 0.8	79 ± 0.1	15 ± 0.5	3 ± 0.1	4.1 ± 0.2	May 1985, Barents Sea
Arctic Cod	13.2 ± 1.3	14.2 ± 4.3	72 ± 0.0	15 ± 0.1	10 ± 0.1	7.4 ± 0.1	February 1985, Svalbard area
B. Guillem: Capelin	9.2 ± 0.4	3.6 ± 0.6	78 ± 0.1	16 ± 0.1	3 ± 0.2	4.5 ± 0.1	March 1986, Barents Sea
Arctic Cod	9.9 ± 2.2	7.7 ± 7.1	77 ± 0.1	15 ± 0.1	5 ± 0.0	4.9 ± 0.0	June 1986, Kongsfjorden

Table 4 Mean nitrogen and energy content (dry mass) of the guano excreted and mean nitrogen retention and assimilation efficiency (± SE) of Kittiwakes and Brünnich's Guillemots when fed capelin and Arctic Cod

	Nitrogen (%)	Energy (kJ/d)	Nitrogen retention (% of BW)	AE (%)	AEn (%)
Kittiwake: Capelin	22.2 ± 0.5 (n = 10)	11.6 ± 0.1 (n = 3)	0.3 ± 0.06	77.5 ± 1.4 (n = 10)	72.2 ± 0.7 (n = 10)
Arctic Cod	20.1 ± 0.6 (n = 8)	12.2 ± 0.2 (n = 3)	0.1 ± 0.03	83.1 ± 0.7 (n = 8)	81.2 ± 0.4 (n = 8)
Br. Guille.: Capelin	21.6 ± 0.6 (n = 9)	12.0 ± 0.1 (n = 3)	0.2 ± 0.05	74.4 ± 1.6 (n = 9)	70.6 ± 0.6 (n = 9)
Arctic Cod	20.6 ± 1.0 (n = 5)	11.7 ± 0.3 (n = 5)	0.2 ± 0.06	78.2 ± 2.5 (n = 5)	74.7 ± 0.9 (n = 5)

is particularly important when working with birds that have a nitrogen retention different from zero, such as growing or fasted birds. This has generally been neglected in seabird assimilation efficiency studies (Jackson 1986).

In our study, correcting for nitrogen retention reduced AE-values by 2–7%. This indicates that the birds were retaining nitrogen, i.e. building up body proteins. They were probably replacing proteins lost during the first days of captivity. They may also have been replacing proteins which are normally lost during the breeding period, especially by females (Gabrielsen et al. 1991b).

In the study of White-chinned Petrel (*Procellaria aequinoctialis*) fledglings, Jackson (1986) found reductions in AE's from 6% to 11% when correcting for nitrogen retention. These birds had a body-mass reduction of 3.8% per day throughout the experimental period (10 days), resulting in a negative nitrogen balance. It is probable that the feed sizes given in this experiment were below maintenance level when combined with the starvation periods carried out. The loss of body-mass was assumed not to affect the result of the experiment. Both nitrogen- and energy metabolism are however affected in starved poultry (Hartel 1986), and starvation is not recommended in poultry feeding experiments. This could also be true in sea bird feeding experiments.

Cause of variation in AEn's

AEn's for both Kittiwakes and Brünnich's Guillemots were highest when they ate Arctic Cod. Although acclimation to one food type may have a short term effect on the utilization of other food types, the possibilities for such error were reduced in the study by a three day acclimation period prior to each trial.

A difference in protein quality is a possible cause for the difference in AEn's between foods (McNab and Shannon 1974). However, it is not likely that this explains the variance in AEn's in this study. Nitrogen assimilation (% nitrogen retained of nitrogen intake) was highest in Kittiwakes when fed Capelin ($p = 0.001$), corresponding to lowest AEn's, while the difference between the two Brünnich's Guillemot trials was not significant ($p = 0.8$). Thus, none of the birds showed a higher assimilation of nitrogen corresponding to the highest AEn values, as would be expected if differences in protein quality were to cause differences in AEn's.

Several studies have shown a considerable seasonal variation in the nutrient composition of Capelin (Jangaard 1974; Eaton et al. 1975; Montevecchi and Piatt 1984). Montevecchi and Piatt (1984) found constant protein (13–14%) content in New-Foundland Capelin all the year around, where as fat and water content varied inversely proportionally. Fat content was highest (18%) in December and lowest (3%) after the spawning period in June–July. Jangaard (1974) describes similar fluctuations for the Barents Sea Capelin, with the minimum value for fat immediately after the fish have spawned in April.

The nutritive difference between the two food types was in their fat content. Capelin had the lowest content of fat (3%), and resulted in the lowest AEn's in both bird species. The Arctic Cod, with 5% and 10% fat, resulted in intermediate and high AEn values in Brünnich's Guillemots and Kittiwakes, respectively. The relationship between fat content of food and AEn's may be linear (Figure 1). This figure indicates that 1) Kittiwakes and Brünnich's Guillemots have the same assimilation efficiency for food items of fish origin with the same fat content, and 2) assimilation efficiency is directly proportional to the fat content of the food. These hypothesis should be subject to further studies.

An addition of fats to poultry diets has become routine primarily to increase the caloric density of the food (Sell and Owings 1981). However, fats also have a lower calorific effect (thermal energy) than other nutrients, and thereby reduce digestive rate and prolong the time for digestion and absorption of other nutrients. The high fat content (10%) of the Arctic Cod fed to Kittiwakes gave a higher energy density in this food than in the low-fat (3%) Capelin. This might explain the abrupt decrease in food consumption (33%) seen in Kittiwakes at the shift in food. A decrease in food intake, though smaller (4%), was also seen in Brünnich's Guillemots at the shift in food, corresponding to an increase in fat content of food from 3% to 5%.

Several scientists (Biely and March 1954; Tochburn and Naber 1966; Jensen et al. 1970; Sell and Owings 1981; Hurwitz et al. 1986; Maiorino et al. 1986) have also reported a higher than expected improvement in the assimilation efficiency by poultry after supplementing their foods with fats. Tochburn and Naber (1966) called this "the extra calorific effect of fat", and it may be caused by a synergism between saturated and unsaturated fatty acids (Mateos and Sell 1980).

Fatty acids from fish are both saturated and unsaturated. In addition to increase the caloric density and lower the calorific effect of the food, it is therefore possible that fat from fish also shows this "extra calorific effect" in seabirds.

Comparing AEn's from different seabird species and foods

AEn's in White-chinned Petrels (Jackson 1986) fed Myctophids (*Maurolicus mülleri*; 69.1%), squid (*Loligo reynaudi*; 68%) and Antarctic krill (*Euphausia superba*; 67.5%) were lower than all AEn's in this study. This may be due to differences in fat content (which are not given), to the differences in chemical structure of the foods, and/or to differences between the bird species.

Jackson's study (1986) of White-chinned Petrels does not present the values of fat content of the different food items. However, energy and nitrogen contents (dry weight) are given, in addition to wet/dry weight ratios. Using a conversion factor of 6.25 between nitrogen and proteins, and assuming that the mean energy content of proteins is 22.59 kJ/g (Whittow 1986), 79% (4.5 kJ/g fish wet weight) of the total energy content of the light fish (Myctophids; 5.7 kJ/g fish wet weight) would be of protein origin. The main energy contributors in fish are fats and proteins. Energy from carbohydrates is negligible. If mean energy content of fish-fat is assumed to be 35.4 kJ/g fat (Brekke and Gabrielsen, unpubl.), then 3% (0.03 g fat/g fish wet weight) of the Myctophids would be fat. Assuming the same values for energy content of protein and fat to hold for squid, 1.3% (1.2 kJ from fat/g fish wet weight) of the squid would be fat. Antarctic krill contains chitin, which makes it difficult to do similar calculations.

Values for estimated fat content and assimilation efficiency from White-chinned Petrels eating Myctophids and squid fit fairly well into Fig. 1. Being aware of the assumptions made above, these calculations still give additional support to the theory that assimilation efficiency is strongly dependent on the fat content of the food, and independent of the species of seabird studied.

Food Consumption

In order to illustrate the applicability of our work on assimilation efficiency on Kittiwakes and Brünnich's Guillemots we present the following example (values have been rounded). Kittiwakes and Brünnich's Guillemots have field metabolic rates of 795 kJ per

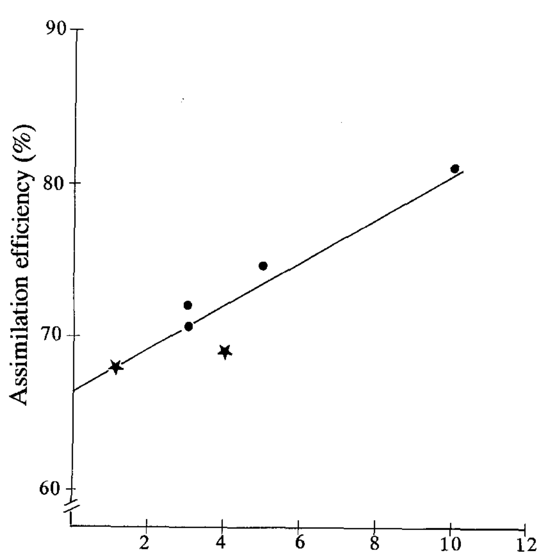

Fig. 1 Relationship between assimilation efficiency (nitrogen corrected) and fat content in foods. Calculated values from Jackson (1986) are included as *. ($AEn = 67.8 + 1.3\,x$, $r^2 = 0.88$, $p < 0.005$)

day and 2080 kJ per day, respectively, when feeding their chicks (Gabrielsen et al. 1987, Flint and Hunt, unpubl.). At this same time of year (July/August), Capelin in the Barents Sea has a fat content of about 12%, corresponding to an energy content of 7.25 kJ/g (Jangaard 1974). The Arctic Cod has a fat content of about 5%, corresponding to an energy content of 4.9 kJ/g (Brekke and Gabrielsen, this paper). Using 84% and 75% assimilation efficiency for Capelin and Arctic Cod, respectively (derived from Fig. 1), gives a metabolizable energy of 6.1 kJ/g of fresh Capelin and 3.7 kJ/g of fresh Arctic Cod, and the birds will have a daily consumption of fish as follows (assuming a diet of only one fish species):

Kittiwake	130 g Capelin/day
	215 g Arctic Cod/day
B. Guillemot	341 g Capelin/day
	562 g Arctic Cod/day

During 30 days of chick rearing (35–40 days in Kittiwakes and 20–22 days in Brünnich's Guillemots) two adults from each species would consume 8 kg Capelin, 15 kg Arctic Cod, 20 kg Capelin or 34 kg Arctic Cod, respectively. The estimated breeding population on Svalbard is 250 000 Kittiwakes and 875 000 pairs of Brünnich's Guillemots (Mehlum and Bakken, in press). These birds would therefore consume 18 500 tons Capelin or 31 600 tons of Arctic Cod during the 30 days they feed their chicks. Of the total energy 16% (or 2.15×10^{10} kJ) and 25% (or 3.87×10^{10} kJ) respectively, is returned to the marine and terrestrial ecosystems in the Svalbard region.

Using the assimilation efficiencies 75% (average; Furness 1978) and 100% (ignoring assimilation efficiency) keeping fat content as above, yields consumptions of Capelin approximately 10% higher and 15% lower, respectively, than in the example above. When considering that the fat content of food varies through out the year, and that assimilation efficiency might vary proportionally to fat content of feed, the amount of food these birds consume may vary broadly throughout the year.

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