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NITROGEN AND CARBON ISOTOPE RATIOS IN SEABIRD ROOKERIES AND THEIR ECOLOGICAL IMPLICATIONS[1]

HIROSHI MIZUTANI AND EITARO WADA
Laboratory of Biogeochemistry and Sociogeochemistry, Mitsubishi-Kasei Institute of Life Sciences, 11 Minamiooya, Machida, Tokyo 194 Japan

Abstract. Various samples around gull and penguin rookeries were examined for nitrogen and carbon isotope ratios. The results showed that input of organic nitrogen from avian breeding activity, followed by its aerobic decomposition in soil and by volatilization of the resultant ammonia, strongly dominated nitrogen flow in both rookeries. Plants, animals, and soils in the rookeries appeared dependent on the nitrogen thus provided.

In the penguin rookery, soil organic carbon was also derived from breeding activity. A large input of organic carbon by gulls, however, appeared to have quickly escaped from the gull rookery through respiration. It had little effect on the soil organic carbon; the main source of organic carbon there seemed to have come from higher plants.

Major pathways of material flow in the seabird rookeries were deduced from the isotopic data. Study of stable isotopes should enable us to draw similar pictures for other ecosystems; it is particularly useful in places where frequent visits are impractical.

Key words: *ammonia volatilization; carbon isotope ratio; food chain; material flow; nitrogen isotope ratio; remote field; rookery; seabird.*

INTRODUCTION

A uniquely luxuriant plant community often forms in seabird rookeries (Ishizuka 1966, Ishizuka et al. 1985). One reason why a seabird rookery supports such a peculiar ecosystem may be a large influx of essential nutrients caused by avian breeding activity. For instance, annual inputs of nitrogen, phosphorus, and potassium to a Black-tailed Gull (*Larus crassirostris*) rookery in Kabushima, Japan, were estimated to be respectively 53 g/m^2, 45 g/m^2, and 21 g/m^2 (Mizutani 1984). These are much more than those to cultivated fields even in countries where the most fertilizer-intensive agriculture in the world is undertaken (Ohtake 1982). This ornithocoprophilous plant community would not exist if the birds were absent.

Though a study on the ecological structure of such a community may be of considerable interest, the usually isolated locations of seabird rookeries make frequent visits impractical. In such cases, study of stable isotopes of bioelements is often useful in elucidating ecological structure (Haines 1976, Fry et al. 1978*b*, Wada 1980, Peterson et al. 1985, Wada et al. 1987*a*). As nitrogen and carbon isotopes integrate information over time, a study of their content in various samples from rookeries could provide an interesting opportunity to elucidate nutrient fluxes in such an ecosystem.

MATERIALS AND METHODS

Sampling locations

Two rookeries were chosen as primary sites for the present study: a Black-tailed Gull (*Larus crassirostris*) rookery in Japan and an Adelie Penguin (*Pygoscelis adeliae*) rookery in Antarctica.

The Black-tailed Gull rookery was Kabushima rookery (40°32′12″ N, 141°33′41″ E) in Hachinohe, Aomori Prefecture, Japan. The rookery was sampled on 1 March, 13–14 May, 9 June, and 21 July 1980, 13 May and 24 July 1981, and 3 August 1986. The breeding season of the gulls varies depending on the year, and is usually from February to August. Narita (1985) gives detailed accounts of the breeding activity and geographical features of the island.

The penguin rookery was at Cape Bird, Ross Island, Antarctica (77°12′ S, 166°28′ E). A shallow pond (≈10 cm at the deepest) was present near the center of the rookery. Chicks of Adelie Penguins form large gatherings from 3 to 8 wk after hatching (Aoyanagi 1981). Samples were obtained on 6 January 1981 (Nakaya et al. 1982), which was a few days before the formation of such gatherings.

In addition to these primary sites, a few samples were collected from two other rookeries. They were a Black-tailed Gull rookery (35°4′48″ N, 132°19′33″ E) in Okihebishima, Yunotsu, Shimane Prefecture, Japan, and a Short-tailed Albatross (*Diomedea albatrus*) rookery (30°29′ N, 140°18′ E) in Torishima, Izu Islands, Japan.

Okihebishima is an uninhabited island, though occasional visits by fishermen and others occur. Plant leaves, surface soils, and gull feathers and droppings were collected there during 8–9 June 1984. Nakai (1981) gives a detailed account of the rookery.

Torishima is a remote, volcanic island located in open ocean ≈580 km south of Tokyo. The volcano is active and has erupted twice in this century (in 1902 and 1939). The only known rookery of the Short-tailed

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Albatross in the world is on this uninhabited island. Volcanic ash soils were collected from the rookery on 25 March, 21–22 June, and 16–17 November 1982. Body feathers of the Short-tailed Albatross were found in the rookery. They were collected on 21 March 1977 and 14 April 1984. The breeding season of the Short-tailed Albatross is from October to May (Hasegawa and DeGange 1982).

Soils and bottom mud

Procedures for preparations of rookery soils and bottom mud in the pond are given elsewhere in detail (Mizutani et al. 1986); they were roughly as follows for the soils from the gull rookeries. Surface soil (0–5 cm) was collected and transferred to a plastic vial. For the study of vertical profile, rookery soil was layered every 5 cm beginning at the surface and going to a depth of 20 cm. Each layer was packed in a stainless-steel cylinder so as not to disturb its original structure. After the soil samples were filled with ethanol, the vials and the cylinders were moved to the laboratory in a refrigerated container. The purpose of the addition of ethanol was to prevent otherwise rapid decomposition of organic matter. The addition did not cause any interference with the isotope analyses. For instance, two ethanol-treated soils from Matsushima (35°4′20″ N, 132°19′14″ E), another rookery of the Black-tailed Gull in Japan, gave the $\delta^{13}C$ value of -17.9 and $-18.9‰$, while two untreated soils from the same two cores yielded the $\delta^{13}C$ value of -18.1 and $-18.8‰$, respectively. (For definition of $\delta^{13}C$, see Isotope Analysis, below.) Upon arrival, the contents were vacuum dried in a Labconco FDC-8 freeze dryer (Labconco Corporation, Kansas City, Missouri, USA), passed through a 2-mm stainless-steel sieve, and then homogenized to pass a 0.5 mm stainless-steel sieve. A small portion of the soil was kept separately without addition of ethanol to obtain its water content.

Excreta

Immediately after collection, the mass of fresh gull droppings was measured, a known amount of ethanol was added, and the container was tightly sealed. After arrival at the laboratory, the container was opened, the contents were vacuum dried, and the dried excreta were crushed in a glass mortar to pass a 0.5 mm stainless-steel sieve.

Fresh penguin excreta were collected soon after their deposition onto the soil surface and kept frozen in a plastic vial. They were later vacuum dried and crushed in the same manner as the gull droppings.

Higher plants

Aerial parts of rape (*Brassica campestris*) and of red fescue (*Festuca rubra*) were collected from Kabushima rookery. Fresh leaves of oleaster (*Elaeagnus umbellata* v. *rotundifolia*) were collected from Okihebishima rookery and from a nearby coastal cliff. The rookery had little vegetation other than a few oleaster trees.

During transport from the rookeries to the laboratory, the plant samples were put in a plastic bag and kept in a refrigerated container. The samples normally reached the laboratory within a day. Upon arrival, they were rinsed with water to remove any foreign materials. They were then vacuum dried, cut with a pair of stainless-steel scissors, further chopped by an analytical mill, and stored in an airtight container. The container was kept in a refrigerated room (4°C) until ready for chemical analyses.

Algae and cyanobacteria

Fresh green algae (*Prasiola cripsa*) were collected from an algal felt in the penguin rookery. Other than cyanobacteria in the rookery pond, the green algae were the only photosynthetic organism found in the rookery. The algae were stored in a plastic vial and kept below 0° until arrival at the laboratory, where they were vacuum dried and subjected to chemical analyses without further treatment.

Aggregates of cyanobacteria were netted from the pond at Cape Bird. Pond water was eliminated by centrifugation. The remaining aggregates were stored in a plastic vial. After freezing, the contents were handled in the same manner as the algae.

Animal and animal remains

Earthworms were collected from rookery soil in Kabushima. They were kept alive within the soil in a plastic container during transport to the laboratory. The soil was washed away with water, and the earthworms were freeze dried. Insects of *Chrysomelidae* sp. were caught by an insect net and put in a plastic vial filled with ethanol vapor. The vial was opened in the laboratory, and the insects were vacuum dried.

Barely digested sardines (*Sardinops melanosticta*) and larvae of the Japan soldier fly (*Stratiomyia* sp.) were collected immediately after they were regurgitated by gulls in Kabushima rookery. They were rinsed with water, put in a plastic container, and transported to the laboratory. During the transport, which took less than a day, they were kept in a refrigerated container.

Mysids (*Gastrosaccus vulgaris*) were netted at a seashore near Kabushima rookery where many gulls were observed to feed. Anchovy (*Engraulis japonica*) and squid (*Todarodes pacificus*) were caught off the coast of Hachinohe. Immediately after collection, mysids, anchovies, and squid were frozen. They were delivered to the laboratory within 2 d.

Once in the laboratory, samples were rinsed with water and freeze dried. The dried larvae were put in a plastic vial and stored in a cold room (4°). The dried sardines, anchovies, squid, and mysids were cut with a pair of stainless-steel scissors into small pieces. They were further chopped by an analytical mill, put in a plastic vial, and stored in a freezer.

TABLE 1. Kjeldahl nitrogen content and its isotope ratio for various samples around bird rookeries.

Sample	N content (mg/g dry sample)			Isotope ratio (δ^{15}N, ‰)		
	No.	Mean ± SD	Range	No.	Mean ± SD	Range
Kabushima (gull rookery)						
Mysids	4	101 ± 5	98.5–108	4	7.3 ± 0.1	7.2–7.4
Anchovy	10	111 ± 14	85.2–123	10	7.9 ± 0.3	7.3–8.4
Squid	5	123 ± 5	114–127	5	9.1 ± 0.7	8.2–10.0
Sardine	4	95.5 ± 26.5	66.6–119	4	11.9 ± 0.1	11.7–12.0
Japan soldier fly, larvae	5	91.3 ± 29.0	52.5–117	5	11.6 ± 0.9	10.3–12.4
Gull feather	7	138 ± 13	118–154	7	12.3 ± 0.4	11.7–12.8
Gull excreta, fresh	4	152 ± 18	132–174	4	9.4 ± 0.8	8.8–10.6
Rookery soil*	35	12.9 ± 9.5	0.8–32.0	34	19.1 ± 2.7	13.6–24.8
Rape	4	35.5 ± 10.3	26.3–48.4	4	16.6 ± 1.7	14.4–18.3
Red fescue	6	22.6 ± 15.4	7.2–47.3	4	15.1 ± 4.4	11.8–21.5
Earthworm	4	93.5 ± 2.4	91.0–96.7	4	25.4 ± 1.2	23.6–26.4
Cape Bird (penguin rookery)						
Penguin*†	11	108 ± 29	37.0–150	13	10.3 ± 1.5	8.3–13.0
Penguin excreta, fresh	5	116 ± 6	112–127	4	8.0 ± 0.4	7.4–8.3
Penguin guano	7	98.4 ± 34.1	38.5–142	6	13.4 ± 4.2	9.3–19.9
Rookery soil*	8	24.6 ± 8.5	11.9–34.2	8	31.8 ± 4.2	26.8–38.1
Pond bottom mud	7	23.1 ± 14.8	9.4–44.2	6	32.4 ± 0.9	31.7–33.7
Algae on rookery soil	4	44.1 ± 7.8	34.2–52.2	4	16.0 ± 5.2	9.7–21.5
Cyanobacteria in pond	5	38.6 ± 5.1	34.5–45.2	5	35.7 ± 1.7	34.1–37.6

* A portion of individual results has been published in Mizutani et al. (1986).
† Penguin organs examined were bone, skin, feather, muscle, heart, and liver.

Many feathers were scattered over the gull rookeries. Fairly dry feathers of adult gulls were obtained and transferred to the laboratory at ambient temperature. They were rinsed and cleaned with water, and then vacuum dried. Body feathers of the Short-tailed Albatross were treated in the same manner as the gull feathers.

Muscles of Adelie Penguins were obtained from two dead bodies found in the rookery at Cape Bird. Some details on these samples are in Mizutani et al. (1986).

Krill (*Euphausia superba*) was obtained from the north of the Weddell Sea near the Scotia Sea. Mysids were collected at Cape Bird. They were kept frozen and treated in the same manner as the Antarctic algae and cyanobacteria.

Penguin guano was sampled in the rookery at Cape Bird by scooping it to an approximately 5 cm depth. After collection, it was treated in the same manner as the penguin excreta.

Determination of Kjeldahl nitrogen content

Organic nitrogen was converted to ammonia by Kjeldahl digestion (Mizutani et al. 1985*a*). The ammonia thus produced was steam distilled and collected in a 0.125 mol/L H_2SO_4 trap. The ammonium sulfate solution was diluted to volume with water in a 100-mL volumetric flask.

The nitrogen content was determined by using an aliquot of the diluted solution, with the remainder used for nitrogen isotopic measurement. The phenol-hypochlorite method (Solorzano 1969) was employed for the determination. Some additional details of the measurement are in Mizutani et al. (1986).

Determination of organic carbon content

A sample was combusted to form carbon dioxide as described elsewhere (Mizutani and Wada 1985*b*). The amount of gas thus generated was measured manometrically. Organic carbon content of the sample was calculated from its volume, and the gas was later used for carbon isotopic measurement.

Isotope analysis

Ammonium sulfate solutions were converted in vacuo to N_2 gas with alkaline hypobromite. The method was a modification of Rittenberg (1946), and Mizutani et al. (1986) gives details of the procedure. The nitrogen gas thus produced was purified by circulating it for 30 min in a line that had a CuO furnace with Pt wire heated at 700° and a Cu furnace heated at 400°. It was then introduced to a Hitachi RMU-6R mass spectrometer with dual inlet and double collector systems for ratiometry. The nitrogen isotope ratio was expressed as deviation from atmospheric nitrogen, in thousandths (‰), as defined by the following equation:

$$\delta^{15}\mathrm{N} = \frac{(^{15}\mathrm{N}/^{14}\mathrm{N})_{\mathrm{sample}} - (^{15}\mathrm{N}/^{14}\mathrm{N})_{\mathrm{air}}}{(^{15}\mathrm{N}/^{14}\mathrm{N})_{\mathrm{air}}} \times 10^3.$$

Working standards were two ammonium sulfate solutions with δ^{15}N of −3.4‰ and 1.3‰. Standard deviation of the nitrogen isotope measurements was 0.2‰.

Stable carbon isotope ratios were measured with the same mass spectrometer. The carbon isotopic data were expressed in the same manner as for nitrogen. In accordance with convention, they are reported as δ^{13}C

relative to the PDB carbonate standard, which is a Cretaceous belemnite (*Belemnitella americana*) from the Peedee Formation of South Carolina. Carbon isotope data were corrected for ^{17}O. Results from a triple-collecting Finnigan MAT-250 of the National Institute of Agrobiological Resources of Japan were compared with those from the Hitachi RMU-6R to modify the correction equation of Craig (1957). Working standards of carbon were calibrated against United States National Bureau of Standards isotope reference material Number 20 and Number 21. The $\delta^{13}C$ values for the two working standards were -19.4 and -12.0‰. Standard deviation of the carbon isotope measurements was 0.1‰.

Results and Discussion

Table 1 shows the content and $\delta^{15}N$ of Kjeldahl nitrogen in various samples around the gull rookery and the penguin rookery. The variation of values for $\delta^{15}N$ given in the table suggests several factors responsible for altering the ratio.

Nitrogen in birds and in their diet

Stable nitrogen isotope ratios of naturally occurring samples vary depending on many factors. A difference in their contribution to individual samples results in a natural variability. Among these factors, a ^{15}N enrichment along a food chain causes a relatively orderly change in $\delta^{15}N$ among organisms in nature.

Miyake and Wada (1967) first reported an enrichment of ^{15}N along a food chain. Their observation was later confirmed both in culture experiments (DeNiro and Epstein 1981) and in marine and terrestrial ecosystems (Schoeninger et al. 1983, Schoeninger and DeNiro 1984). The enrichment was found among most prey–predator relationships regardless of trophic level, habitat, form of excreted nitrogen, and growth rate. The extent of the enrichment, however, appeared variable. Examining 26 pairs of prey–predator relationships in various habitats, Minagawa and Wada (1984) reported an average ^{15}N enrichment of 3.4‰ for one feeding process with a standard deviation of 1.1‰. Recently, Wada et al. (1987*b*) obtained through a linear regression analysis involving four trophic levels an enrichment factor of 3.3‰ between prey and predators for Antarctic food webs.

Feathers of adult Black-tailed Gulls had $\delta^{15}N$ of 12.3‰ (Table 1). The value may be considered representative for the whole body since $\delta^{15}N$ values for feathers of the Adelie Penguin are similar to the average of its other organs (Mizutani et al. 1986). Our personal observations of >10 species of birds (including the Black-tailed Gull) having various dietary requirements in captivity and of two species of hummingbirds and one species of petrel in the wild also indicate that the $\delta^{15}N$ values of feathers are not much different from those of the birds' other organs (H. Mizutani et al., *personal observations*). If this similarity in $\delta^{15}N$ also holds in the case of wild gulls, average $\delta^{15}N$ for adult gulls' diet is estimated to be $\approx$9‰.

K. Narita (*personal communication*) reports that sardine, anchovy, mysids, and squid account for most of the diet of adult Black-tailed Gulls. They, however, constitute little more than half of the diet of the chicks; nearly half comes from larvae of the Japan soldier fly (S. Wada 1923, Narita 1985). The estimated value of 9‰ for the diet of adult gulls coincides with the simple average of the ratios for their reported foods (9.1‰) and excludes the possibility that the adult gulls continue to feed mostly on larvae of the Japan soldier fly.

The enrichment factor of $\approx$3.3‰ (Wada et al. 1987*b*) indicates that the $\delta^{15}N$ of the diet of Adelie Penguins must, on the average, be $\approx$7‰. The penguins at Ross Island feed mostly on krill, while small fish and copepoda are less important (Aoyanagi 1981). Six analyses of the krill yielded the $\delta^{15}N$ of 4.2‰ with a standard deviation of 0.7‰. E. Wada (*personal observation*) found that six small fishes (body size ranging from 80 to 198 mm; average 156 mm) obtained beneath the Ross Ice Shelf near the McMurdo Base of the United States have a $\delta^{15}N$ value of 14.8‰ with a standard deviation of 0.9‰. A sample of copepoda from the same area yielded a $\delta^{15}N$ value of 15.7‰. These results suggest that isotopically distinct groups contribute to the penguin diet, with krill as its major component. A simple material balance shows that krill could constitute three-fourths of their diet, which agrees well with the field observation.

Because of the enrichment of ^{15}N in avian bodies, their droppings should show a depletion of ^{15}N. Our earlier study of the Black-tailed Gull and the Adelie Penguin excreta showed that the nitrogen isotope ratio for uric acid, the predominant form of metabolized nitrogen in their droppings, was very similar to that of the whole excreta (Mizutani et al. 1985*a*, *b*), though organic nitrogen in urine and that in feces of cattle were reported to have different nitrogen isotope ratios (Steele and Daniel 1978). The earlier study reported four analyses of whole gull droppings from Kabushima rookery. They yielded a mean $\delta^{15}N$ of 9.2‰ and a standard deviation of 0.4‰, while $\delta^{15}N$ for uric acid alone averaged 9.1‰ with a standard deviation of 0.4‰ (Mizutani et al. 1985*a*). Therefore, the nitrogen isotope ratio for droppings may be considered the same as that of the metabolized nitrogen. The $\delta^{15}N$ values for excreted nitrogen of the penguins and the gulls are, then, statistically not different from the estimated ratios of their diets. This may be because the overall rate of ^{15}N accumulation is not rapid enough for adult gulls and penguins to manifest a significant depletion of ^{15}N in their excreta.

Nitrogen after deposition

After the deposition of droppings onto the rookery soil, nitrogen in them undergoes various processes. Nitrogen in other materials such as avian carcasses, food

remains, and feathers will be exposed to similar processes. Although wind, rain, and seawater spray would remove some of these materials from the rookery, much may remain and become subject to ecogeochemical transformations. For instance, uric acid deposited onto Kabushima rookery soil undergoes microbial conversion to ammonia (Mizutani and Wada 1985*a*).

Kjeldahl nitrogen of soil in the rookeries exhibited a considerably higher $\delta^{15}N$ than that for incoming material of avian origin. Other sources of nitrogen such as precipitation and in situ dinitrogen fixation do not cause the high ratio, because the $\delta^{15}N$ values for nitrogen from these sources are $\approx 0‰$ (Wada et al. 1975, Peters et al. 1978).

Nitrogen isotope fractionation associated with the volatilization of ammonia causes the isotope ratio for the remaining nitrogen to be elevated (Kirshenbaum et al. 1947). Mizutani et al. (1986) reported that the high ratio for rookery soils is due to isotope fractionation during ammonia volatilization. A laboratory experiment on uric acid decomposition using Kabushima rookery soil demonstrated the enrichment process of ^{15}N in soil (Mizutani et al. 1985*a*). At the beginning, 1 g of wet soil (water content: 50%) contained 10 mg of uric-acid nitrogen whose $\delta^{15}N$ was 15.8‰. The soil contained ≈ 14 mg of other forms of Kjeldahl nitrogen. After a 10-d incubation, three-fourths of the uric acid decomposed. The $\delta^{15}N$ for Kjeldahl nitrogen in dried soil increased from 18.7 to 27.1‰, while no change was observed in the isotope ratio for uric acid nitrogen. Ammonia in the dried soil had the $\delta^{15}N$ of 45.2‰. The $\delta^{15}N$ for ammonia evolved from the soil during the incubation was $-3.8‰$.

Once the $\delta^{15}N$ of available nitrogen for photosynthetic organisms in the rookeries becomes high, their tissues may get enriched in ^{15}N. In fact, red fescue and rape in the gull rookery and cyanobacteria in the penguin rookery indicate their use of ^{15}N-enriched nitrogen. The large standard deviations of the $\delta^{15}N$ values for these organisms may reflect a local variability of the isotope ratio for available nitrogen. In fact, the nitrogen isotope ratios for soils and guano also have a relatively large standard deviation. This, in turn, suggests that the series of processes that enriches soils in ^{15}N is locally heterogeneous.

The $\delta^{15}N$ for the green algae in the penguin rookery was not as high as the one for the cyanobacteria. This may be because the algae that grow on the surface of the soil incorporate nitrogen from two sources: one of avian origin and the other of glacial origin. Wada et al. (1981) reported that nitrate in Antarctic soil is extremely depleted in ^{15}N. The large standard deviation of the nitrogen isotope ratio for the algae would have resulted from a local heterogeneity in the utilization of the two sources.

Leaves of oleaster from Okihebishima rookery and from a nearby coastal cliff yielded additional evidence for the uptake of ^{15}N-enriched nitrogen. The $\delta^{15}N$ for leaves from Okihebishima rookery was 8.3‰, while that for the leaves from the coastal cliff outside the rookery was $-1.8‰$ (average of two different trees). The nitrogen isotope ratio for the soils near the oleaster tree in the rookery was 9.1‰, and that outside the rookery was $-4.6‰$. Many *Elaeagnus* plants fix atmospheric dinitrogen, and the oleaster is likely to have such an ability. Biological dinitrogen fixation results in organic nitrogen whose $\delta^{15}N$ is $\approx 0‰$. It is unknown how much of the large supply of nitrogen rich in ^{15}N is taken up by the nitrogen-fixing plants in the rookery. However, the 10‰ difference between the two groups of oleaster leaves indicates that a significant portion of nitrogen of the plant in the rookery comes from the ^{15}N-enriched nitrogen.

The ^{15}N-enriched plants and other biological and abiological processes eventually result in the ^{15}N enrichment of soil organic matter. Mizutani et al. (1986) examined the nitrogen isotope ratios for Kjeldahl and ammonium nitrogens in soils of the two rookeries. Their analyses of 18 soil samples from Kabushima rookery gave the $\delta^{15}N$ of $20.4 \pm 2.5‰$ for Kjeldahl nitrogen and that of $31.1 \pm 8.4‰$ for ammonium nitrogen. Two sets of analyses of Cape Bird soils yielded the nitrogen isotope ratio of $32.9 \pm 1.1‰$ for Kjeldahl nitrogen and that of $44.5 \pm 7.2‰$ for ammonium nitrogen. If soil organic and ammonium nitrogens are supposed to constitute soil Kjeldahl nitrogen, their results show that the $\delta^{15}N$ of organic nitrogen in Kabushima soil is $17.3 \pm 2.1‰$ and that in Cape Bird $29.2 \pm 2.0‰$. The value for Kabushima soil is slightly higher than the values for the plants there, and that for Cape Bird soil is in between those for the two photosynthetic organisms present within the rookery. This indicates that most of the soil organic matter is not deposited avian excreta, but is the product of processes subsequent to their deposition.

The earthworms yielded the highest mean $\delta^{15}N$ for Kabushima samples (25.4‰). The effect of ^{15}N enrichment along a food chain must have contributed to the high ratio. Earthworms eat organic detrita in soils whose $\delta^{15}N$ could be as high as 25‰. Chrysomelid beetles in Kabushima rookery showed a $\delta^{15}N$ of 17.5‰. Since they feed on plant leaves whose $\delta^{15}N$ is $\approx 16‰$ (Table 1), it agrees with the enrichment of ^{15}N along a food chain.

Carbon in birds and in their diet

Table 2 shows the content and $\delta^{13}C$ of organic carbon in various samples around the gull and the penguin rookeries. Although it is yet to be established, there are several reports that suggest a slight increase ($\approx 1‰$ or so) in $\delta^{13}C$ of a predator relative to its prey (DeNiro and Epstein 1978, Fry et al. 1978*a*, 1984, McConnaughy and McRoy 1979, Rau et al. 1983, Fry and Sherr 1984). Mizutani (1986) reported an even greater enrichment of ^{13}C in avian feathers; the $\delta^{13}C$ for feathers of the gulls in Kabushima rookery is $\approx 3‰$ higher

TABLE 2. Organic carbon content and its isotope ratio for various samples around bird rookeries.

Sample	C content (mg/g dry sample)			Isotope ratio ($\delta^{13}C$, ‰)		
	No.	Mean ± SD	Range	No.	Mean ± SD	Range
Kabushima (gull rookery)						
Mysids	4	362 ± 2	360–363	4	−18.2 ± 0.2	−18.4–−18.0
Anchovy	7	373 ± 11	358–388	6	−18.6 ± 0.3	−19.1–−18.1
Squid	5	419 ± 20	385–435	5	−19.1 ± 0.9	−20.8–−18.5
Sardine	6	494 ± 59	428–559	6	−22.8 ± 0.4	−23.3–−22.2
Japan soldier fly, larvae	4	423 ± 28	387–452	5	−17.8 ± 1.9	−19.8–−16.0
Gull feather	7	442 ± 21	401–457	7	−16.6 ± 0.3	−17.0–−16.3
Gull excreta, fresh	5	221 ± 7	213–232	5	−19.4 ± 0.6	−19.9–−18.6
Rookery soil	10	88.5 ± 49.5	5.8–175	10	−23.2 ± 1.0	−24.9–−21.3
Rape	9	365 ± 83	247–442	9	−25.4 ± 0.6	−26.9–−24.9
Red fescue	4	414 ± 17	391–432	4	−13.3 ± 0.3	−13.6–−12.9
Earthworm	6	376 ± 106	271–517	6	−21.1 ± 0.9	−21.9–−19.9
Cape Bird (penguin rookery)						
Penguin*	9	261 ± 82	104–343	11	−25.2 ± 0.7	−26.7–−24.3
Penguin excreta, fresh	6	210 ± 17	184–235	10	−28.4 ± 0.6	−29.1–−26.9
Penguin guano	4	118 ± 48	70.2–161	5	−28.1 ± 0.2	−28.4–−27.8
Rookery soil	6	50.2 ± 26.2	25.4–93.6	7	−27.9 ± 0.6	−28.9–−27.1
Pond bottom mud	5	26.0 ± 4.7	18.7–31.1	4	−28.1 ± 1.1	−29.2–−26.9
Algae on rookery soil	4	221 ± 60	131–259	5	−18.7 ± 2.3	−21.5–−17.0
Cyanobacteria in pond	7	136 ± 78	54.3–272	4	−30.3 ± 0.4	−30.7–−29.9

* Penguin organs examined were bone, skin, feather, muscle, heart, and liver.

than the simple average of those for the constituents of adult diet: mysids, anchovy, squid, and sardine. The carbon isotopic difference between the average diet and the droppings is 0.3‰ and statistically insignificant.

As for penguin diet, two analyses of the krill resulted in the $\delta^{13}C$ of −26.6 ± 0.7‰. Mysids obtained at Cape Bird yielded the $\delta^{13}C$ values of −28.5 and −27.8‰. Three of the six fishes at the Ross Ice Shelf averaged −26.0‰ with a standard deviation of 2.0‰. If krill constitutes three-fourths of the penguin diet, the rest being provided equally by small fishes and mysids, the weighted average of the $\delta^{13}C$ for the penguin diet would be −26.7‰, while the $\delta^{13}C$ for the penguin bodies is −25.2‰ (Table 2).

Carbon after deposition

After its deposition onto the rookeries, organic carbon begins to decompose in the soil. Carbon dioxide, a final product of decomposition, will escape from the rookery. Unlike the decomposition and escape of organic nitrogen, there is little overall fractionation in carbon (Wada 1984). Therefore, the $\delta^{13}C$ in rookery soil should roughly equal that of incoming organic matter.

The ratio for penguin rookery soil in Table 2 shows that nearly all organic carbon in the rookery soil originated from the deposition of organic matter by the breeding birds. Photosynthetic algae contributed only a negligible amount of organic carbon. The scarcity of vegetation within the rookery and the cold climate of Antarctica must have caused the accumulation of organic matter of predominantly avian origin, though various processes after deposition might have transformed its chemical nature. In fact, the accumulation is apparent because of the formation of hills rich in organic matter around the nesting areas.

This is not the case for the gull rookery. Instead, there is a difference of almost 4‰ between the droppings and the soil. Rape gives the closest value to soil organic matter among three possible carbon sources (excreta, rape, and red fescue). Rape is the dominant plant species in the island (Kikuchi 1916, Ishizuka 1966). Another major rookery plant, red fescue, had a $\delta^{13}C$ >10‰ higher than that of rape.

The ratio for the rape is typical for terrestrial C_3 plants, while that for the red fescue is representative of C_4 plants (Bender 1971, Smith and Epstein 1971, Benedict 1978, Mizutani and Wada 1985*c*). If a mixture of the three different sources (i.e., C_3 plants, C_4 plants, and avian droppings) is to explain the carbon isotope ratio for the soil organic matter, the organic carbon from C_3 plants must account for at least 63%. The actual contribution of C_3 plants is likely to be much higher, because the minimum number assumes no contribution from the red fescue, which is unrealistic. Therefore, the avian droppings must account for much less than 37% of the soil organic carbon. The large input of organic matter through the breeding activity has little influence on the $\delta^{13}C$ for soil organic matter in the gull rookery. It may indicate that organic matter from the avian activity decomposes faster than that of plant origin.

The change in the $\delta^{13}C$ with depth in the rookery soil confirms this observation. The top layer (0–5 cm depth) showed the $\delta^{13}C$ of −21.3 and −21.4‰ (two analyses). The bottom layer (15–20 cm depth) gave the ratio of −25.4 and −25.5‰ (two analyses). The $\delta^{13}C$ for the two layers in between the top and the bottom was

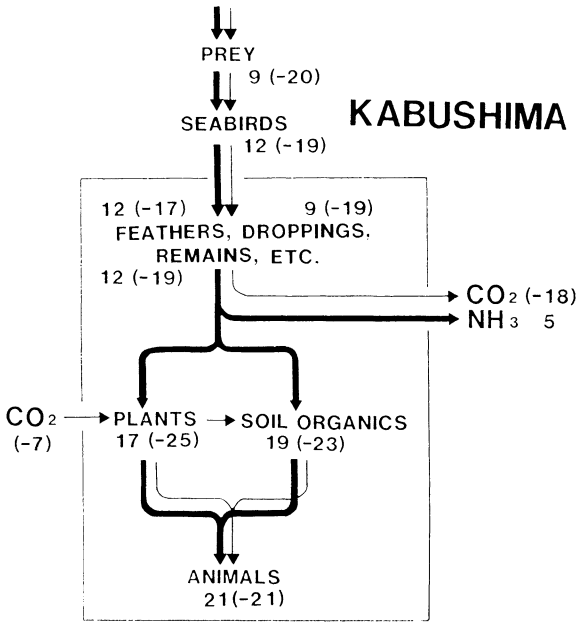

FIG. 1. Major pathways of nitrogen and carbon around Kabushima rookery. Thick arrow indicates flow of nitrogen, and thin arrow stands for flow of carbon. The rectangle indicates the area of the rookery. Only major pathways estimated by the isotope ratios are shown. Soil organics include ammonium nitrogen. Animals feed on either plants or soil organics within the rookery. Numbers show nitrogen and carbon isotope ratios for each component in the rookery. Those without parentheses are $\delta^{15}N$ values and those in parentheses $\delta^{13}C$ values. If there are several trophic levels among animals in the rookery, their nitrogen and carbon isotope ratios would be different from those shown and determined by the food chain effects discussed in the text.

-25.2 (5–10 cm depth) and -25.4‰ (10–15 cm depth). The values at the top are close to that for the droppings, and the values for the other three layers are close to the one for the rape. With only the top layer being different, the vertical profile of isotope ratios for soil ammonium nitrogen in a Black-tailed Gull rookery showed a similar pattern (Mizutani et al. 1986). Together with the quick aerobic decomposition of uric acid in Kabushima surface soil, these results must indicate a highly active decomposition of avian organic matter at the surface of the rookery soils. The ^{15}N enriched soil organic matter, whose $\delta^{15}N$ is similar to those for the rape and the red fescue, also suggests quick decomposition and a large contribution from the plants to the soil organic matter in Kabushima. Therefore, most soil organic carbon that has a long half-life in soils of the gull rookery must be of plant origin.

In the case of Torishima, 1 g of the dried rookery soil contained only 4.3 ± 0.7 mg of organic carbon, whose $\delta^{13}C$ was -20.1 ± 0.1‰ (five analyses). The $\delta^{13}C$ for feathers of the Short-tailed Albatross was -16.6 ± 0.6‰ (two analyses), which suggests $\delta^{13}C$ of ≈ -19.4‰ for its excreta. Although a few plant species such as the composite *Chrysanthemum pacificum* and a eulalia (*Miscanthus condensatus*) are present in the Torishima rookery (Kabaya 1982), vegetation in the colony of the Short-tailed Albatross is very scarce (Hasegawa and DeGange 1982, Hasegawa 1985). Because of this, the organic carbon present in very low concentrations in the rookery soil may have a $\delta^{13}C$ similar to that of avian origin.

The $\delta^{13}C$ for Okihebishima soils averaged -22.6‰ with a standard deviation of 1.0‰ (four analyses). The rookery had two possible sources of organic carbon: the Black-tailed Gull and the higher plants (C_3 plants). Leaves of the oleaster tree gave the $\delta^{13}C$ of -26.1‰. Two analyses of gull feathers yielded the $\delta^{13}C$ of -18.8 and -15.8‰. The $\delta^{13}C$ of gull droppings was -17.9‰. Contributions of allochthonous and autochthonous organic carbon seem nearly equal in the rookery.

It is possible that changes in vegetation occur so rapidly in a seabird rookery that casual observations may be insufficient for estimating an extent of contribution to material flows by various ecogeochemical agents. In fact, the vegetation in a Black-tailed Gull rookery, Fumishima (35°26′38″ N, 132°37′46″ E), changes drastically enough to surprise an infrequent visitor (Nakai 1962, Ishizuka 1966). Carbon isotope study should be of great value to such a sporadic observer in assessing the extent of contributions from different sources because (1) most soil organic matter has a half-life of much longer than a year (Jenkinson and Rayner 1977) and (2) the carbon isotope ratio for soil organic matter faithfully reflects that of its source, its change during early diagenesis being minimal (Mizutani and Wada 1982).

CONCLUSIONS

The present isotopic study elucidates major pathways of material flow in seabird rookeries and associated ecogeochemical processes.

Inorganic nitrogen inputs through precipitation and in situ dinitrogen fixation were relatively unimportant processes in the rookeries. Lindeboom (1984) noted that nitrification and denitrification were apparently minor in the nitrogen flow in penguin rookeries. Our personal observations indicate that the same may be true of gull rookeries. Instead, microbial degradation of organic nitrogen of avian origin and volatilization of the resultant ammonia were quantitatively the most important processes.

The volatilized ammonia may provide nitrogen for a rich plant community outside the rookery. Heavy rains and predominantly westerly winds in rookeries of Macaroni Penguins (*Eudyptes chrysolophus*) of Marion Island (46°54′ S, 37°44′ E) produce an "ammonia shadow" around the rookeries, where rich vegetation and peat layers are present (Lindeboom 1984). Since the source of nitrogen in the peat layers must have been volatilized ammonia from the rookeries, it may be speculated that the $\delta^{15}N$ of the peat must be ex-

tremely low. Consequently, a study of the change in the ratio with depth into peat layers that are >6 m thick should be of considerable interest. Such a study might provide an historical insight into processes that have eventually resulted in their formation.

While most soil organic nitrogen was of avian origin for the rookeries examined, soil organic carbon was not always so. Most soil organic carbon was autochthonous in Kabushima rookery, and it was dominantly allochthonous in the penguin rookery and the albatross rookery. In seabird rookeries where a rich ornithocoprophilous plant community forms, nitrogen would be allochthonous and carbon autochthonous.

Fig. 1 schematically shows the major nitrogen and carbon pathways in the Kabushima gull rookery. The $\delta^{15}N$ and $\delta^{13}C$ for the prey are the mean of the four constituents of adult diet. The nitrogen and carbon isotope ratios for feathers and droppings are those given in Tables 1 and 2, while $\delta^{15}N$ and $\delta^{13}C$ for the gulls and their remains are an estimate based on the 3.3‰ enrichment for nitrogen and the 1‰ enrichment for carbon. No fractionation of carbon isotopes is assumed during the respiration and the loss of carbon dioxide (Wada 1984). The $\delta^{15}N$ for volatilized ammonia is estimated from the results obtained through a laboratory decomposition experiment using Kabushima rookery soil (Mizutani et al. 1985*a*). The values for plants are those of rape, since C_4 plants appear to play only a minor role. The $\delta^{13}C$ for incoming CO_2 is that of atmospheric carbon dioxide. "Soil organics" stands for the Kjeldahl nitrogen of rookery soil in Table 1 and for soil organic carbon in Table 2. The nitrogen and carbon isotope ratios for animals are the averages for the insects ($\delta^{15}N$ given earlier in the text and $\delta^{13}C = -20.1$‰), which feed on plant leaves, and for the earthworms (Tables 1 and 2), which live on soil organic matter.

Fig. 2 shows the major pathways in the penguin rookery. The $\delta^{15}N$ and $\delta^{13}C$ for penguins, their droppings and remains, algae, and cyanobacteria are those given in Tables 1 and 2. The nitrogen and carbon isotope ratios for prey are estimated from those for penguins based on the enrichments along a food chain. The values for feathers are from the results of actual feather analyses ($\delta^{15}N = 8.8$‰ for chick tailfeather; $\delta^{15}N = 10.8$‰ and $\delta^{13}C = -25.1$‰ for juvenile body-feather). The isotope ratios for escaping carbon dioxide and ammonia were estimated in the same manner as for Kabushima rookery. Soil organics signify the same as in Fig. 1. There is an uncertainty whether the source of carbon for the algae is atmospheric carbon dioxide, bicarbonate, or both. Although the algae were exposed to the air at the time of sampling, Fig. 2 assumes algal utilization of bicarbonate. Table 2 gives a large standard deviation of $\delta^{13}C$ for the algae. This may be due to the difference among the algae in their utilization of the two carbon sources. They may take up bicarbonate either from water in the soil or by growing in the water.

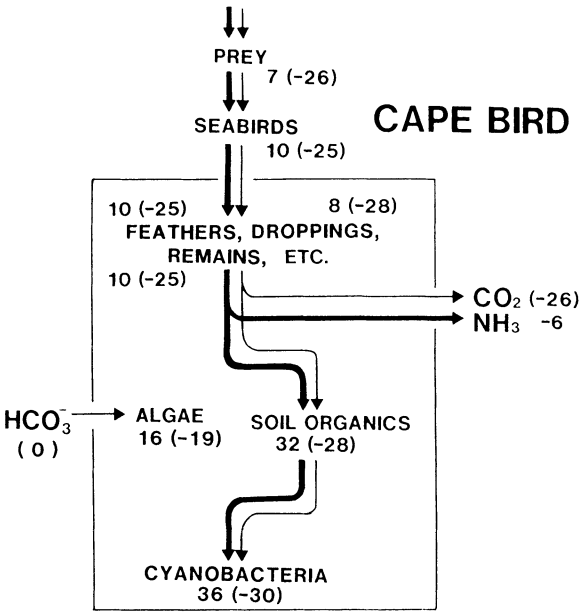

FIG. 2. Major pathways of nitrogen and carbon around the penguin rookery at Cape Bird. Notations are the same as in Fig. 1. Cyanobacteria live in the pond, whose bottom mud showed nitrogen and carbon isotope ratios similar to those for the rookery soils.

The patterns of carbon and nitrogen flows in Kabushima and Cape Bird rookeries seem to represent two different types of material flow in seabird rookeries. Absolute values of the isotope ratios change depending on the isotope ratios and the combination of the sources of organic matter and on other factors. However, relative relationships between two components in most seabird rookeries would be somewhere in between those in these two rookeries. Though organic contents differ, the pattern of the flows of nitrogen and carbon in Torishima rookery would be more like the one in the penguin rookery. Higher plants, carbon dioxide, and animals in Torishima rookery will replace algae, bicarbonate, and cyanobacteria, respectively, in Fig. 2. Okihebishima rookery appears to stand midway between Kabushima and Cape Bird.

As seabirds often nest in a place far from the nearest human habitation, the access of researchers to such a rookery is very limited. An isotopic study might prove particularly useful in obtaining ecogeochemical relationships in such ecosystems.

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