농학석사 학위논문

Foraging habits of Gentoo and Chinstrap penguins revealed by stable isotope analysis on King George Island, Antarctica

킹조지섬에 서식하는 젠투펭귄과 턱끈펭귄의 안정성 동위원소를 이용한 식이 습성 연구

2013 년 8 월

서울대학교 대학원

산림과학부 산림환경학전공

강 화 연

Foraging habits of Gentoo and Chinstrap penguins revealed by stable isotope analysis on King George Island, Antarctica

킹조지섬에 서식하는 젠투펭귄과 턱끈펭귄의 안정성 동위원소를 이용한 식이 습성 연구

지도교수 이 우 신

이 논문을 농학석사 학위논문으로 제출함.
2013년 8월

서울대학교 대학원
산림과학부 산림환경학전공
강 화 연

강화연의 농학석사 학위논문을 인준함.
2013년 8월

위 원 장 _____ (인)

부위원장 _____ (인)

위 원 _____ (인)

Abstract

Foraging habits of Gentoo and Chinstrap penguins revealed by stable isotope analysis on King George Island, Antarctica

Hwa-yeon Kang
Major in Forest Environmental Sciences
The Graduate School
Seoul National University

The ecology of diving seabirds is largely affected by the abundance and distribution of the marine prey community. Determining various foraging habits of different species is important for understanding seabird species as indicators of a changing environment, and the management and conservation of the seabird species. In this study, I used two stable isotopes, ^{13}C and ^{15}N, in the whole blood of Chinstrap (*Pygoscelis antarctica*) and Gentoo penguins (*Pygoscelis papua*). The primary intent of this study is to investigate intra- and inter-specific differences at the trophic level and origin of the penguin diet. To explain the differences in foraging habits and diets due to sexual size dimorphism, I analyzed the morphological characteristics of adult males and females. I also identified the foraging areas of Chinstrap penguins with global

positioning system (GPS) loggers. Whole blood samples were collected for stable isotope analysis from the 13th of January until the 6th of February, 2013. During this period, the penguin chicks were in the late guarding and early crèching stages. At the time of blood sample collection, flipper length, foot length, bill length to the feathering, bill depth, head length and body mass of the adults were also measured. To track the foraging trips of Chinstrap penguins, five GPS loggers were attached to ten adult birds from the 10th of January until the 7th of February, 2013. As a result, the trophic levels for Chinstrap and Gentoo penguins did not differ. However, Chinstrap penguins appeared to forage in more offshore areas in comparison to Gentoo penguins. The males for both species were larger than the females, especially in the bill size. The males showed a higher trophic level than females for both species. However, there was no significant difference in foraging areas between males and females as indicated by $\delta^{13}C$. According to the isotope comparisons for age, chicks showed lower $\delta^{15}N$ values than the adults for both species. The finding suggests that adults feed their chicks with prey in the lower trophic level in comparison to their own diet. Chicks also had lower $\delta^{13}C$ values. Thus, adults extract prey from more offshore areas for their chicks.

Keywords: Dietary variation, King George Island, *Pygoscelis antarctica*, *Pygoscelis papua*, sexual dimorphism, stable isotope

Student number: 2011-23499

Table of Contents

List of Tables

List of Figures

Ⅰ. Introduction

Seabirds occupy an indispensable part of the marine ecosystem (Croxall 1987; Hobson and Welch 1992), and are controlled by the abundance, distribution and composition of prey species (Montevecchi and Myers 1995). Seabirds can be indicators of changing ecosystem health and food web structure (Newman et al. 2007; Iverson et al. 2007). Hence, it is necessary to understand the factors that influence the population dynamics of seabirds by studying their diet and foraging behavior (Montevicchi 1993).

When two species are similar in general ecological preferences and coexist in an overlapping habitat, they must have different realized niche to decrease interspecies competition (MacArthur 1958; Hardin 1960; Miller et al. 2010). Competition and specialization between species influence the structure of seabird colonies, and the behavior of each species (Ainley et al. 2003b). It is important to understand the interspecific differences in foraging habits of marine predators in order to understand their responses to environmental change (Croxall et al. 1999).

Strong intraspecific competition also influences the foraging behaviors in colonial seabirds (Lewis et al. 2001). Sexual dimorphism in size, which is widespread among colonial seabirds, allows each sex to catch different prey items

(Selander 1972; Warham 1972; Forero et al. 2002; Forero et al. 2005; Miller et al. 2010; Dehnhard et al. 2011; Michalik et al. 2013).

Another form of intraspecific diet specialization appears between the adults and their chicks. For a faster growth and higher survival rate, chicks need a lot of energy and high quality diet (Massias and Becker 1990; Starck and Ricklefs 1998). Prey with higher lipid and protein contents are generally considered to be suitable for chicks (Clarke and Prince 1980; Hislop et al. 1991; Anthony et al. 2000). Several Antarctic and sub-Antarctic seabird species including Antarctic fulmarine petrels, Magellanic penguins (*Spheniscus magellanicus*), Southern giant petrels (*Macronectes giganteus*), and Yellow-eyed penguins (*Megadyptes antipodes*) have been reported to provide their chicks selectively on prey, which are easier to digest and have higher nutritional value (Hodum and Hobson 2000; Forero et al. 2002; Forero 2005; Browne 2011).

Given the importance of diet in inter- and intra-species competition, stomach content analysis has been conventionally used to determine diets of seabirds (Croxall et al. 1980; Croxall and Lishman 1987; Kokubun et al. 2010; Miller et al. 2010; Polito 2011). Stomach content analysis is useful to identify and measure the major prey items as long as the content is not digested too much (Duffy and Jackson 1986). However, stomach content analysis has certain limitations since it can simply show the information of one foraging trip (Duffy and

Jackson 1986; Gales and Cheal 1992; Tierney et al. 2008), and may be biased because of different digestive rates for diverse prey items (Jackson and Ryan 1986; Jackson et al. 1987).

More recently, stable isotope analysis became a common tool to replace or compensate conventional methods that investigate diet and trophic structures (e.g., Hodum and Hobson 2000; Forero et al. 2002; Polito et al. 2011; Browne et al. 2011). Researchers can minimize potential damage to the birds by taking a small amount of blood, feathers or egg membranes for diet and trophic studies (e.g., Bearhop et al. 2002; Brasso 2012). Stable isotope analysis is based on the fact that the stable isotope ratio of consumer tissues changes in a predictable way, depending on prey items (DeNiro and Epstein 1978; 1981). The ratio of heavy nitrogen isotope ^{15}N increases by 3–5 parts per thousand (‰) along each trophic level as more amounts of lighter isotope ^{14}N excreted with the uric acid in birds (DeNiro and Epstein 1981). On the other hand, the ratio of ^{13}C is affected by primary production process rather than the trophic level, resulting in a lower ^{13}C ratio in pelagic diets compared to benthic or inshore diets (Hobson et al. 1994).

The stable isotope signature for each tissue reflects integrated dietary information of a certain period of time according to its turnover rate (Hobson and Clark 1992). Whole blood, which was used in this study, represents diets for the last four weeks before the analysis (Hobson and Clark 1992),

and is therefore suitable for a diet study during the chick-rearing period (Forero et al. 2002).

In this study, blood samples of Chinstrap and Gentoo penguins breeding on King George Island are collected for stable isotope analysis. The objective of this study is to investigate inter- and intra-specific segregation in diets and foraging ranges of the two penguin species. In detail, the study focuses on the three following hypotheses:

1. There is a difference in diet and foraging ranges between the two sympatric breeding Chinstrap and Gentoo penguins.
2. As the two species show sexual dimorphism in size, males are expected to catch larger prey and thus occupy a higher trophic level.
3. Adults are expected to feed their chicks with different prey from their own diets because chicks require higher nutritional demands.

Ⅱ. Literature review

1. Concept of stable isotope use in dietary studies

Isotopes are forms of the same element with a different number of neutrons. Stable isotopes are isotopes that are not radioactive and persist in the same form forever. Stable isotopes are abundant in nature and can be useful tracers of element cycling. Heavy and light isotopes have almost identical chemical properties, but subtle differences in reaction rate affect the distribution of isotopes (Fry 2006).

In the case of nitrogen stable isotopes, because of the faster loss of ^{14}N in metabolism and excretion (DeNiro and Epstein 1981; Fry 2006), ^{15}N shows stepwise enrichment with increasing trophic level. ^{15}N has been used to study trophic relationships among seabird species (Hobson 1993; Hobson et al. 1994; Sydeman et al. 1997; Thompson et al. 1999).

Composition of carbon stable isotopes is affected by primary producers, which the food web is based on (Fry 2006). According to a study by France (1995), the average $\delta^{13}C$ value for marine phytoplankton was −22 ‰ in comparison to −17 ‰ for marine benthic algae. Since an inshore ecosystem is based more on benthic algae while an offshore ecosystem is based more on marine phytoplankton, inshore marine organisms are more enriched in ^{13}C than offshore marine organisms

(France 1995). Consequently, marine predators that feed on the inshore areas have higher ^{13}C values than the offshore foragers (Cherel and Hobson 2007).

Stable isotope ratios can be used to quantify the relative proportion of different food items in the consumer diet by applying isotopic mixing model when the isotopic values of each component are known. The simplest models use only one isotope with two dietary sources, or a dual isotope with three dietary sources (Phillips and Gregg 2001). More advanced methods are not limited by the number of sources, but the multi-source mixing models have lower resolution than simple models (Phillips and Gregg 2003).

2. The ecology of pygoscelid penguins

Genus *Pygoscelis* includes three penguin species: Adelie (*P. adeliae*), Chinstrap (*P. antarctica*), and Gentoo (*P. papua*). All three species breed in colonies (Davis and Renner 2003). Pygoscelid penguins have circumpolar distribution. However, Gentoo penguins breed on sub-Antarctic islands and the Antarctic Peninsula. Adelie and Chinstrap penguins breed south of the Antarctic convergence. Non-breeding distribution for all species are poorly known (Williams 1995). In the study of sympatrically breeding Adelie, Chinstrap and Gentoo penguins, all three species primarily fed on Antarctic krill *(Euphausia*

superba), but Gentoo penguins consumed more fish, primarily *Pleurogramma antarcticum* (ca. 15% of meal mass). The Chinstrap and Gentoo penguins fed almost exclusively on krill (more than 99% of meal mass) (Volkman et al. 1980). Chinstrap penguins also consume fish and other species of crustaceans when possible (del Hoyo et al. 1992). Gentoo penguins have the most northern distribution among the three species (Davis and Renner 2003), and fed more on fish (83%), primarily *Nototheniops larseni* and *Champsocephalus gunnari*. This is specific for male Gentoo during the nonbreeding season. (Williams 1991). Referencing the study on foraging trip patterns, Gentoo penguins fed deep and inshore, whereas Adelie and Chinstrap penguins fed shallow and offshore, reducing potential competition by different breeding time from early to late summer (Trivelpiece et al. 1987; Kokubun et al. 2010). In addition, Chinstrap and Gentoo penguins spent more time for feeding and traveling. The average time for feeding dive (128s) for Gentoo penguins was longer than Chinstrap penguins (91s) (Trivelpiece et al. 1986).

Sexual size dimorphism appears in Gentoo (Stonehouse 1970), Chinstrap (Amat et al. 1993), and Adelie penguins (Ainley and Emison 1972), where males are larger than females. The stomach contents of the male compared to the female Gentoo (Williams 1991) and Adelie penguins (Clarke et al. 1998) consisted of more fish, and the males of the Gentoo penguin had a higher trophic level than females (Bearhop et al.

2006). Meal mass from the stomach of males and females were not different for the Gentoo penguins, but were similar or larger in males of the Chinstrap penguin (De Leon et al. 1998; Miller et al. 2010). Males and females of Chinstrap penguins traveled similar distances from the shore. However, in the case of Gentoo penguins, the sex which traveled greater distance was reversed by the study site (Miller et al. 2010). The foraging trips of female Adelie penguins were longer and greater in distance than males (Clarke et al. 1998).

Stable isotope analyses have also been used to investigate the ecology of pygoscelid penguins. Some research used nitrogen and carbon isotope ratios of Adelie (Mizutani and Wada 1998; Dunton 2001) and Chinstrap penguins (Dunton 2001) to study material flow and food web structure of Antarctic fauna. Stable isotopes were also used to evaluate spatial and temporal variation of diet between colonies of Adelie penguins (Ainley et al. 2003a), and sex-specific foraging habits of diving seabird species including Gentoo penguins (Bearhop et al. 2006). To quantify the diets of Chinstrap and Gentoo penguins, Polito et al. (2011) compared and integrated stable isotope analysis with stomach content analysis. Although there were several diet studies using stable isotopes for pygoscelid species, little information about inter- and intra-specific diet segregation is available for sympatric breeding penguins.

Ⅲ. Materials and methods

1. Study area

This study was conducted at Narebski Point (62°14' S, 58°46' W), designated as an Antarctic Specially Protected Area (ASPA) No. 171, in the Barton Peninsula on King George Island, South Shetland Islands, Antarctica (Figure 1). This area has an annual average temperature of −1.8℃ (maximum 9.8℃, minimum −23.1℃), total precipitation of 597.2mm and mean wind velocity of 7.1m/s (KOPRI and Ministry of Environment 2009). This area is covered with snow for most of the year, except for a short period in the summer. The main vegetation for this area is composed of mosses and lichens, mostly *Sanionia chorisodontium* and *Usnea himantormia* respectively, which are tolerant of extensively dry conditions and the extreme cold weather of Antarctica (Seppelt et al. 1995). Compare to relatively bare land environments, the nutrient−rich water of the Antarctic Ocean supports the Antarctic food web (Davis and Renner 2003). The Euphausiid crustaceans including Antarctic krill are extremely abundant in cold polar oceans (Shirihai 2002).

Every austral summer, a large number of Chinstrap and Gentoo penguins breed together in this area with a few breeding Brown skuas (*Stercorarius antarcticus*), South polar

skuas (*Catharacta maccormicki*), Snowy sheathbills (*Chionis albus*), Antarctic terns (*Sterna vittata*), Kelp gulls (*Larus dominicanus*), Southern giant petrels, and Wilson's storm-petrels (*Oceanites oceanicus*) (Ministry of Environment 2007). The breeding population sizes of Chinstrap and Gentoo penguins in the study area are about 3,000 and 2,000 pairs, respectively (Ministry of Environment 2007; 2012). Colonies of Gentoo penguins are small and located in gentle slopes, and flat areas or ridges. On the other hand, Chinstrap penguins form large colonies and prefer rocky, steep areas adjacent to the seashore (Figure 2).

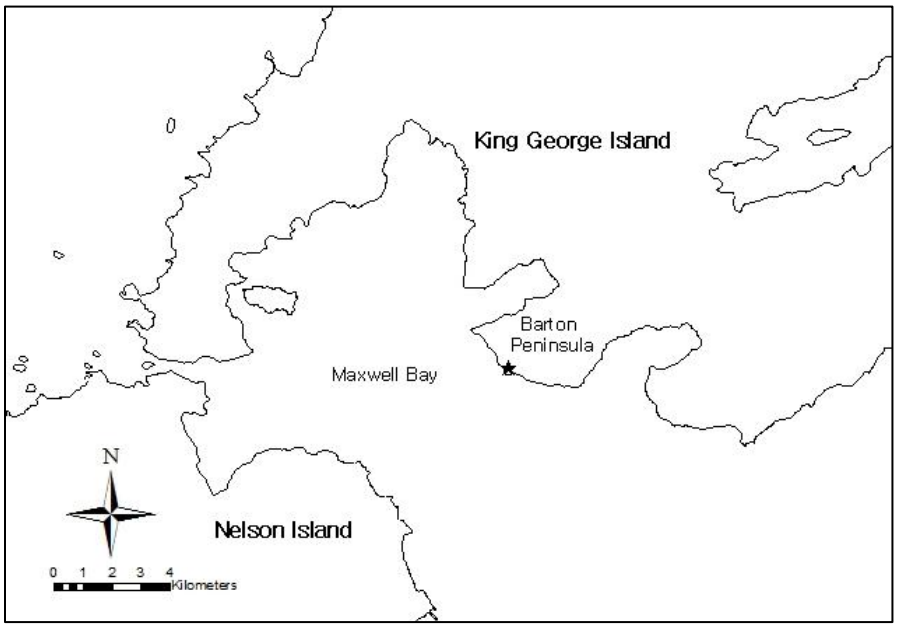


Figure 1. Study area on King George Island. Breeding site (★) is marked

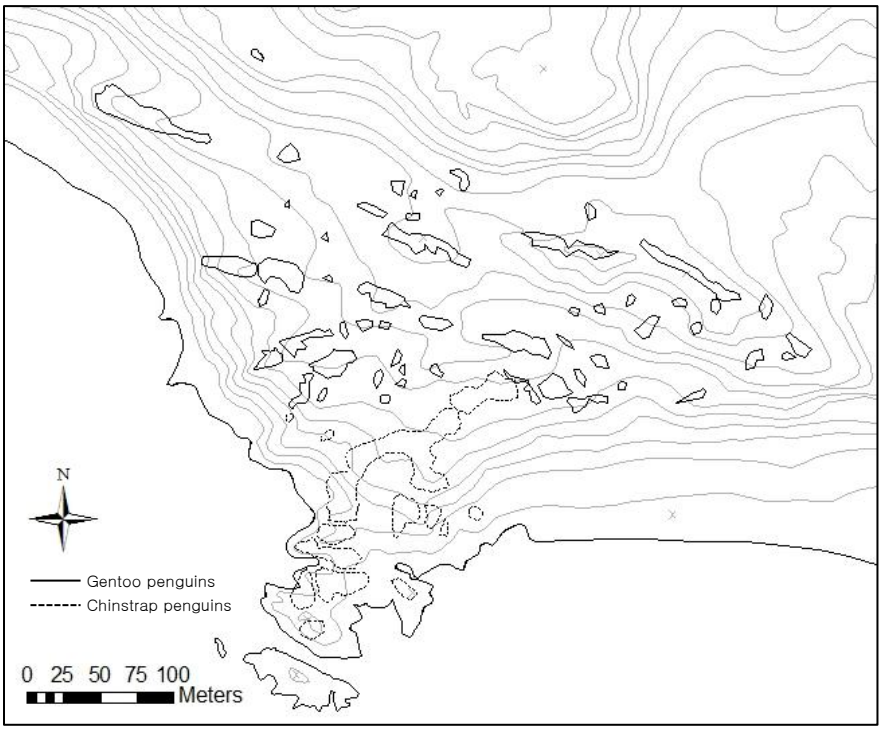


Figure 2. Breeding colonies of Gentoo and Chinstrap penguins

2. Sample collection and measurement

A small amount of whole blood (ca. 0.1 ml) was collected from the brachial vein of the adults and the tibial vein of the chicks (CCAMLR 1984) with disposable syringes. Breeding adults were caught when they had just returned to the colony from the foraging trip. The chicks were caught at the nest or crèching site. The collection date for the adult penguins was between the 13th of January and the 6th of February (2013), from the middle to the end of the guarding stage. The mean hatching dates were the 24th and 28th of December (2012) for the Gentoo and Chinstrap penguins. All samples of the chicks were collected on the 1st of February when the chicks started crèching. Among the collected samples, 17 females, 9 males and 6 chicks from the Chinstrap penguins, and 17 females, 12 males and 6 chicks from the Gentoo penguins were used for stable isotope analysis (Table 4). The flipper length from axillar to tip, foot length, head length, bill length from tip to feathering, bill depth at the posterior edge of the nostril and body mass of adult birds were measured at the time of the sample collection (Figure 3). Measurements of 32 adult Chinstrap penguins and 30 adult Gentoo penguins were used for morphological analysis. Discriminant function (Polito et al. 2012) was used to determine sex of all adults (Table 1). A size dimorphism index (DI: Storer 1966, Ainley and Emison 1972) was determined for each measurement:

$$DI = \frac{100 \text{ x (mean of females} - \text{mean of males)}}{\frac{1}{2}(\text{mean of females} + \text{mean of males)}}$$

A negative value for DI indicates that males are larger. As recommended by Storer (1966), the cube root of the weight was used to allow comparison with the linear measurement.

Every investigation of this study was conducted with permission from the 'Act on Antarctic Activities and Environmental Protection' of the Republic of Korea, and carried out in accordance with the 'SCAR Code of Conduct for the use of Animals for Scientific Purposes in Antarctica.'

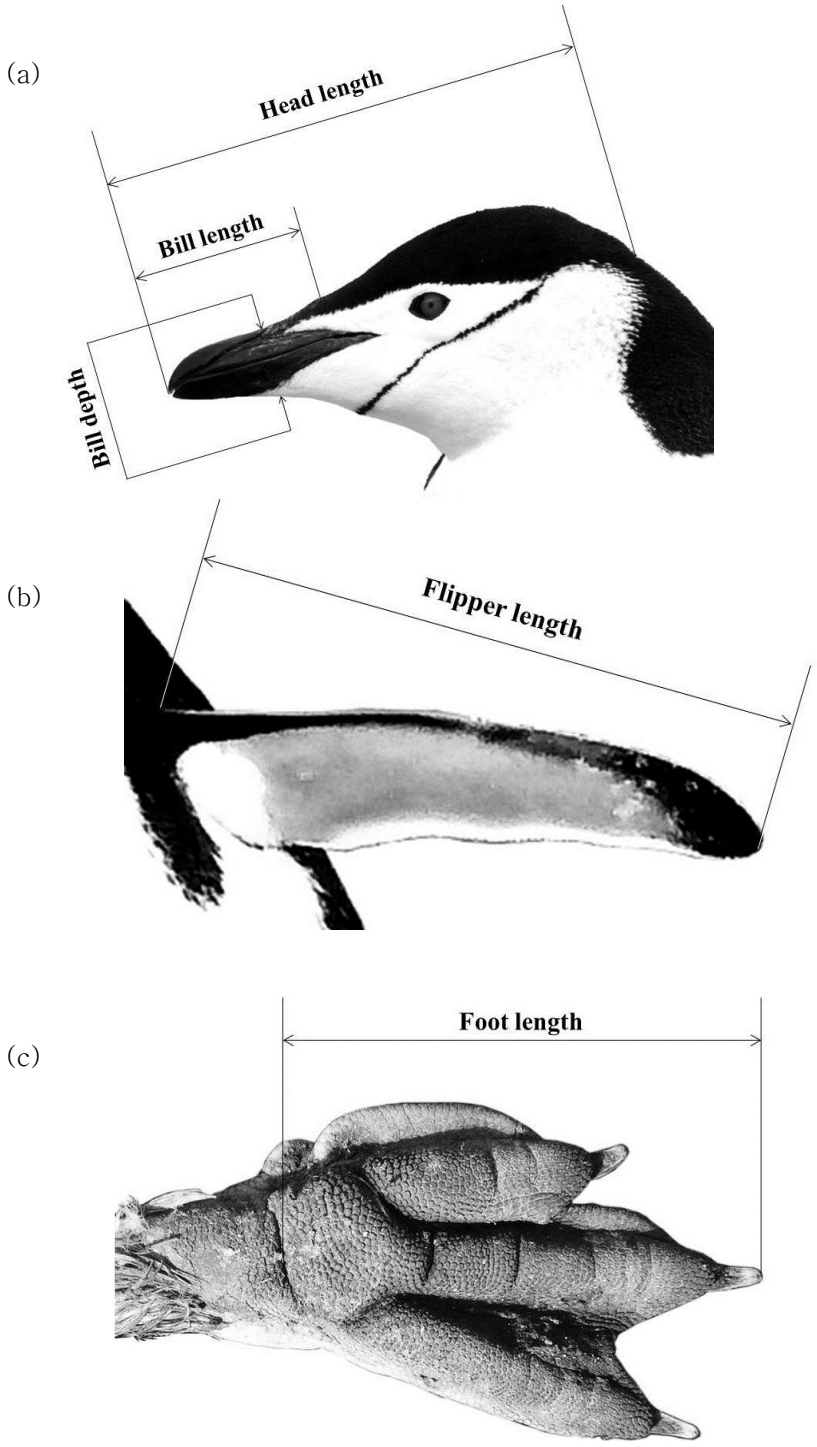


Figure 3. Measurement of penguin body size: (a) measurements of head parts, (b) flipper length, and (c) foot length

Table 1. Morphological sex discrimination of Chinstrap and Gentoo penguins used in this study (Polito et al. 2012)

Species	Discriminant score (D)[a]	Posterior probability of being male	Classification accuracy (cross-validated)[b]
Chinstrap penguin (adult)	D = 120.25754 − 4.10985BD − 0.87985BL	$= \frac{1}{1 + exp(\mathrm{D} - 0.000053)}$	96.7 % (96.7 %)
Gentoo penguin (adult)	D = 53.19063 − 1.89275BD − 0.47576BL	$= \frac{1}{1 + exp(\mathrm{D} - 0.000231)}$	91.7 % (83.2 %)

a Bill measurements (mm): BD = bill depth, BL = bill length, BW = bill width
b Percentage of correct classifications before and after (in parentheses) "leave-one-out" cross-validation.

3. Sample preparation and stable isotope analysis

A total of 67 blood samples from two different species and three different sex/age groups was collected and analyzed for stable isotope ratios. Whole blood samples were oven-dried for at least 72 hours at 60 ℃, and afterwards, stored at room temperature. Lipids were not removed because blood generally has very low lipid component (Deuel Jr. 1955). Samples were powdered with porcelain mortars and pestles for homogenization before the stable isotope analysis. Stable isotope ratios of carbon and nitrogen were analyzed using continuous-flow stable isotope ratio mass spectrometer (IsoPrime-EA, Micromass, UK) linked with a CN analyzer (NA Series 2, CE Instruments, Italy), at the National Instrumentation Center for Environmental Management (NICEM) at Seoul National University. The stable isotope ratios were expressed in δ notation as parts per thousand (‰), according to the following equation:

$$\delta X\ (‰) = [(R_{sample}/R_{standard}) - 1] \times 1{,}000$$

where X is ^{15}N or ^{13}C and R is the corresponding ratio of $^{15}N/^{14}N$ or $^{13}C/^{12}C$, and the $R_{standard}$ is the international standard carbonate Pee Dee Belemnite (PDB) and atmospheric (AIR) nitrogen. Multiple replicate analyses showed that standard deviations for the $\delta^{13}C$ and $\delta^{15}N$ measurements were < 0.1 ‰ and 0.2 ‰, respectively (Hauck 1982).

Two-source isotopic mixing model based on $\delta^{15}N$ values (Phillips and Gregg 2001) was used to estimate the relative proportions of two major prey types (krill and fish) of the Chinstrap and Gentoo penguin diet. In a two-endmember linear mixing model, the mean proportion of source A in the consumer diets can be calculated by the following equation:

$$P_a = (D_t - D_b)/(D_a - D_b)$$

where P_a is the proportion of source A in the consumer diet, and D_t represents the mean $\delta^{15}N$ values of estimated diet of the consumer adjusted from the blood $\delta^{15}N$ value based on the isotopic fractionation factor. I assumed that the isotopic fractionation factor for $\delta^{15}N$ between the diet and whole blood of penguin to be 2.75 ‰ (Cherel et al. 2005). D_a and D_b represent the $\delta^{15}N$ values of source A and B, respectively. In this study, Antarctic silverfish (*Pleuragramma antarcticum*) ($\delta^{15}N$ = 9.4±0.5 ‰, n = 30), which is a commonly found fish species in the diet of Pygoscelid penguins, and Antarctic krill (*Euphausia superba*) ($\delta^{15}N$ = 3.3±0.6 ‰, n = 40) were used as the two representative prey species (Polito et al. 2011). Since the two species are segregated more by $\delta^{15}N$ values than by $\delta^{13}C$ values, ^{15}N was used as single isotope variation in this two-endmember linear mixing model.

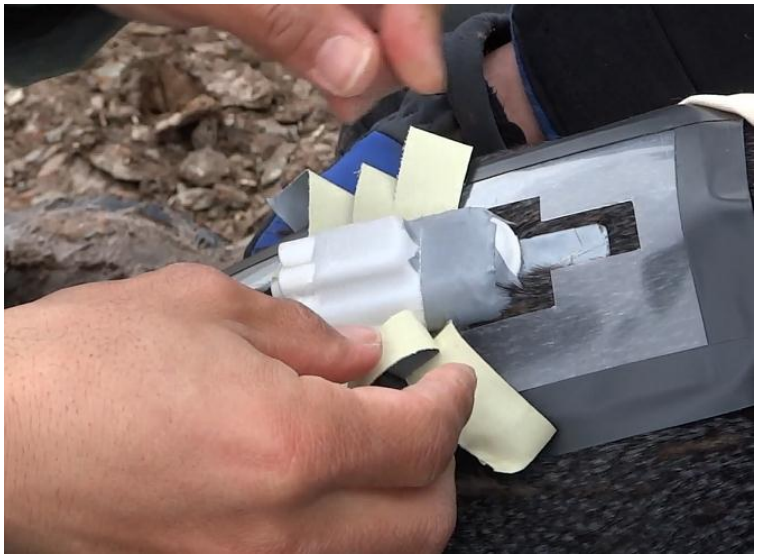
The proportions for each prey species with a 95 % confidence interval for the isotopic model were calculated by Phillips and Gregg (2001).

4. GPS tracking of Chinstrap penguins

Five EP-3.4 global positioning system (GPS) loggers (50 g, 68 mm x 35 mm x 22 mm; Ecotone Inc., Gdynia, Poland) were used to track the foraging trips of 10 Chinstrap penguins from the 10th of January (2012) until the 7th of February (2013). Adult birds were caught at the nest site when their partners had returned from their foraging trip. All tagged penguins were measured and sexed by the discriminant function (Polito et al. 2012). The GPS loggers were attached by the wrapping method with waterproof Tesa tapes (No. 4651; Beiersdorf AG, Hamburg, Germany) (Wilson et al. 1997) on the lower back of the penguins (Figure 4).

Location and diving data were downloaded by radio link through EP BS-12T base station (Ecotone Inc., Gdynia, Poland) every 2-3 days. The raw data were filtered and calculated to trip lengths by individual and sex. The tagged penguins were recaptured after 12-15 days of tracking and the GPS loggers were removed. However, two females were not found in the colony afterwards. Tracking data of 91 foraging trips (44 from five females and 47 from four males) were successfully downloaded and analyzed.

(a)



(b)

Figure 4. Attaching GPS logger: (a) wrapping method with waterproof Tesa tape, and (b) GPS logger on the lower back of an adult Chinstrap penguin

5. Statistical analysis

T-test and Mann-Whitney rank sum test were performed to examine differences in morphological features and trip length between the males and females of Chinstrap and Gentoo penguins. Two-way analysis of variance (2-way ANOVA) was used to investigate differences for species and sex/age groups together on $\delta^{15}N$ values. In the case of $\delta^{13}C$ value, the separation between species was tested by Mann-Whitney rank sum test. Afterwards, one-way ANOVA and Kruskal-Wallis one-way ANOVA on ranks were conducted to determine the differences between sex/age groups within each species of Chinstrap and Gentoo penguins. Shapiro-Wilk test and Levene's test were used to assess the normality of distributions and variance homogeneity, respectively. When there was a significant difference with sex/age groups and no interaction effect between two variables, Holm-Sidak's and Dunn's multiple comparisons were conducted between males, females and chicks. SigmaPlot 12.0 (Systat Software, Inc., CA, USA) was used for all statistical analyses.

Ⅳ. Results

1. Morphological characteristics

In Chinstrap penguins, flipper length ranged from 174.5 to 205.0 mm, foot length ranged from 83.00 to 98.53 mm, bill length was 41.40 to 53.13mm, bill depth was 15.36 to 21.05 mm, head length was 120.14 to 138.76 mm, and body mass was 3.47 to 4.92 kg (Table 2). In the case of Gentoo penguins, flipper length ranged from 198.0 to 230.0 mm, foot length ranged from 84.00 to 101.31mm, bill length was 40.30 to 53.01 mm, bill depth was 13.86 to 17.92 mm, head length was 127.58 to 147.10 mm, and body mass was 4.70 to 7.80 kg (Table 3).

In both species, all body size measurements were significantly larger for males than females, indicating an obvious degree of sexual size dimorphism. In particular, the bill depth was the most dimorphic parameter, followed by the bill length. The least dimorphic feature was the body mass (Table 2, Table 3).

Table 2. Body measurements of Chinstrap penguins (Mean±SD) on King George Island

	Males	Females	Test statistics	p	DI
Flipper length (mm) (range)	198.15±3.51 (192.0−205.0)	188.88±5.52 (174.5−199.0)	t = −5.191	< 0.001	−4.79
Foot length (mm) (range)	91.63±3.95 (84.83−98.53)	87.32±3.36 (83.00−96.04)	U = 42.000	0.002	−4.82
Bill length (mm) (range)	50.11±2.02 (46.08−53.13)	45.24±2.25 (41.40−48.87)	t = −6.062	< 0.001	−10.21
Bill depth (mm) (range)	19.77±0.79 (18.80−21.05)	17.55±0.93 (15.36−19.26)	t = −6.831	< 0.001	−11.90
Head length (mm) (range)	134.31±2.44 (129.25−138.45)	127.94±4.66 (120.14−138.76)	U = 33.000	< 0.001	−4.86
Body mass (kg) (range)	4.39±0.44 (3.56−4.92)	3.96±0.3 (3.47−4.60)	t = −3.187	0.002	−3.44
N	13	19			

Table 3. Body measurements of Gentoo penguins (Mean±SD)

	Males	Females	Test statistics	p	DI
Flipper length (mm) (range)	219.73±7.61 (205.5−230.0)	210.89±5.63 (198.0−221.0)	t = 3.527	< 0.001	−4.11
Foot length (mm) (range)	94.35±3.57 (87.52−101.31)	89.36±3.18 (84.00−94.56)	t = 3.868	< 0.001	−5.43
Bill length (mm) (range)	48.94±2.39 (44.91−53.01)	43.91±2.11 (40.30−49.57)	t = 5.846	< 0.001	−10.83
Bill depth (mm) (range)	17.07±0.63 (16.05−17.92)	15.13±0.83 (13.86−16.64)	t = 6.666	< 0.001	−12.05
Head length (mm) (range)	141.62±4.25 (132.30−147.10)	133.8±3.61 (127.58−141.63)	t = 5.226	< 0.001	−5.68
Body mass (kg) (range)	6.05±0.53 (5.28−6.92)	5.49±0.74 (4.70−7.80)	U = 46.000	0.009	−3.24
N	12	18			

2. Stable isotope values

2.1 Carbon stable isotope values

In whole blood samples of Chinstrap and Gentoo penguins, $\delta^{13}C$ values ranged from −25.2 to −28.43 ‰ (Table 4, Figure 5). However, there was a significant difference by species on $\delta^{13}C$ values ($U = 86.500$, $p < 0.001$), suggesting that the two penguin species use different sources of the food webs in marine ecosystems. In particular, $\delta^{13}C$ in Gentoo penguins ranged from −27.78 to −25.2 ‰, having a higher value than the Chinstrap penguins, which ranged from −28.43 to −27.11 ‰. There were also differences by sex/age group for both species (Table 5). Adult males and females of both species showed higher $\delta^{13}C$ values than their chicks, but the difference between males and females was not significant (Table 6, Table 7).

Table 4. Stable isotope values (mean±SD) of Chinstrap and Gentoo penguins

	$\delta^{13}C$ (‰) Mean±SD (range)	$\delta^{15}N$ (‰) Mean±SD (range)	N
Chinstrap penguins	**−27.72±0.34 (−28.43 ~ −27.11)**	**7.65±0.42 (6.70 ~ 8.40)**	**32**
Males	−27.56±0.21 (−27.99 ~ −27.21)	8.03±0.24 (7.69 ~ 8.40)	9
Females	−27.67±0.35 (−28.41 ~ −27.11)	7.56±0.40 (6.70 ~ 8.08)	17
Chicks	−28.08±0.18 (−28.43 ~ −27.87)	7.32±0.18 (7.05 ~ 7.49)	6
Gentoo penguins	**−27.02±0.44 (−27.78 ~ −25.20)**	**7.73±0.47 (6.62 ~ 9.17)**	**35**
Males	−26.87±0.58 (−27.36 ~ −25.20)	8.05±0.44 (7.33 ~ 9.17)	12
Females	−26.99±0.25 (−27.29 ~ −26.32)	7.65±0.30 (7.06 ~ 8.24)	17
Chicks	−27.44±0.26 (−27.78 ~ −26.96)	7.34±0.55 (6.62 ~ 8.22)	6

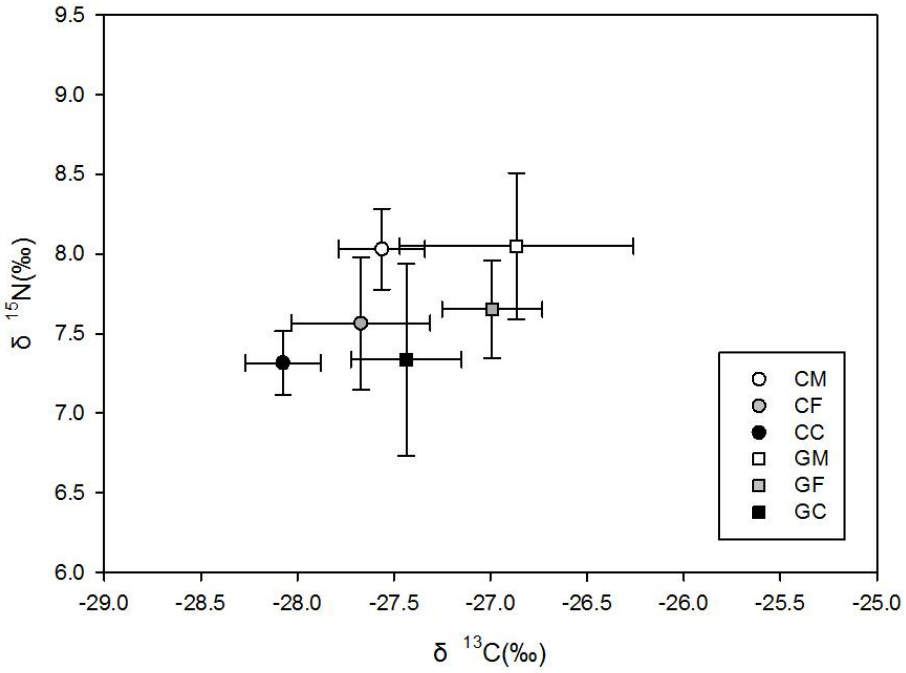


Figure 5. Mean stable isotope values with SD, from whole blood samples of the two penguin species. Circles indicate Chinstrap Penguins (*Pygoscelis antarctica*) while boxes represent Gentoo Penguins (*Pygoscelis papua*). CM, CF, and CC denote males (n = 9), females (n = 17), and chicks (n = 6) of Chinstrap Penguins, whereas GM, GF, and GC denote males (n = 12), females (n = 17), and chicks (n = 6) of the Gentoo Penguins, respectively

Table 5. Comparison between sex/age groups on $\delta^{13}C$ values of Chinstrap and Gentoo Penguins

Source of Variation	DF	SS	MS	Test statistics	p
Sex/Age in Chinstrap p.	2	1.017	0.509	F = 5.562	0.009
Sex/Age in Gentoo p.	–	–	–	H = 9.033	0.011

Table 6. Multiple comparison of $\delta^{13}C$ values between sex/age groups of Chinstrap Penguins

Comparison	Diff. of Means	t	p
Male vs. Chick	0.512	3.210	0.010
Female vs. Chick	0.404	2.812	0.017
Male vs. Female	0.108	0.865	0.394

Table 7. Multiple comparison of $\delta^{13}C$ values between sex/age groups of Gentoo Penguins

Comparison	Diff. of Ranks	Q	p<0.05
Male vs. Chick	13.375	2.611	Yes
Female vs. Chick	14.064	2.890	Yes
Male vs. Female	0.689	0.178	No

2.2 Nitrogen stable isotope values

In whole blood samples of Chinstrap and Gentoo penguins, $\delta^{15}N$ ranged from 6.62 to 9.17 ‰ (Table 4, Figure 5). In the case of the $\delta^{15}N$ value, only sex/age groups had a statistically significant effect, while there was no significant difference between Chinstrap and Gentoo penguins (Table 8). Interaction between species and sex/age was also not significant. Thus, multiple comparisons between males, females and chicks had been conducted regardless of the species. All three groups of males, females and chicks were significantly different from each other (Table 9). On the other hand, juveniles, which are completely dependent on parental care, showed the lowest $\delta^{15}N$ values for both species.

Results from the two-source isotopic mixing models indicated that in Chinstrap and Gentoo penguins, krill composed the majority of the diet of chicks (79.2 % and 78.9 %), and accounted for a gradually less proportion for females (75.2 % and 73.8 %) and males (67.5% and 67.2%), without notable differences between species (Table 10).

Table 8. Two-way ANOVA table on $\delta^{15}N$ values of Chinstrap and Gentoo Penguins by species and sex/age factor

Source of Variation	DF	SS	MS	F	p
Species	1	0.0254	0.0254	0.17	0.682
Sex/Age	2	4.337	2.169	14.5	<0.001*
Species x Sex/Age	2	0.0197	0.00987	0.066	0.936
Residual	61	9.124	0.15		
Total	66	13.601	0.206		

Table 9. Multiple comparisons of $\delta^{15}N$ values between sex/age groups in Chinstrap and Gentoo penguins

Comparison	Diff. of Means	t	p
Male vs. Chick	0.714	5.085	<0.001
Male vs. Female	0.431	3.993	<0.001
Female vs. Chick	0.283	2.179	0.033

Table 10 Estimated diet composition of Chinstrap and Gentoo penguins, derived from nitrogen isotope analysis using the two-source mixing model

	δ^{15}N two-source model	
	% Krill	% Fish
Chinstrap penguins	73.8 (70.3-77.2)	26.2 (22.8 -29.7)
Males	67.5 (63.9-71.2)	32.5 (28.8-36.1)
Females	75.2 (71.2-79.3)	24.8 (20.7-28.8)
Chicks	79.2 (75.5-82.8)	20.8 (17.2-24.5)
Gentoo penguins	72.5 (68.9-76.0)	27.5 (24.0-31.1)
Males	67.2 (62.2-72.2)	32.8 (27.8-37.8)
Females	73.8 (70.4-77.2)	26.2 (22.8-29.6)
Chicks	78.9 (69.3-88.4)	21.1 (11.6-30.7)

3. Foraging trip of Chinstrap penguins

For supportive interpretation of the diet use revealed by stable isotope analysis, foraging trips of Chinstrap penguins, believed to be pelagic foragers, were tracked by GPS loggers. Among the tracking data of 91 foraging trips, 22 trips of four females and four males were not included in the analysis since those trips were not apparent foraging trips and had very short movements from 2.9 to 18.7 km.

The mean foraging trip length of tracked Chinstrap penguins was 59.1±25.9 km (mean±SD), ranging from 23.8 to 133.8 km (Figure 8). The mean trip length of each sex was 64.3.1±27.4 km (n = 35, range: 23.8−133.8 km) in females (Figure 6) and 53.7±23.3 km (n = 34, range: 26.9−129.2 km) in males (Figure 7). No individual difference for each sex was detected in the foraging trips of females (df = 4, F = 0.654, p = 0.992) and males (df = 3, H = 4.153, p = 0.245). There was also no sexual differences in the length of foraging trips (U = 448.0, p = 0.079), referring that the foraging area was not clearly separated between the males and females.

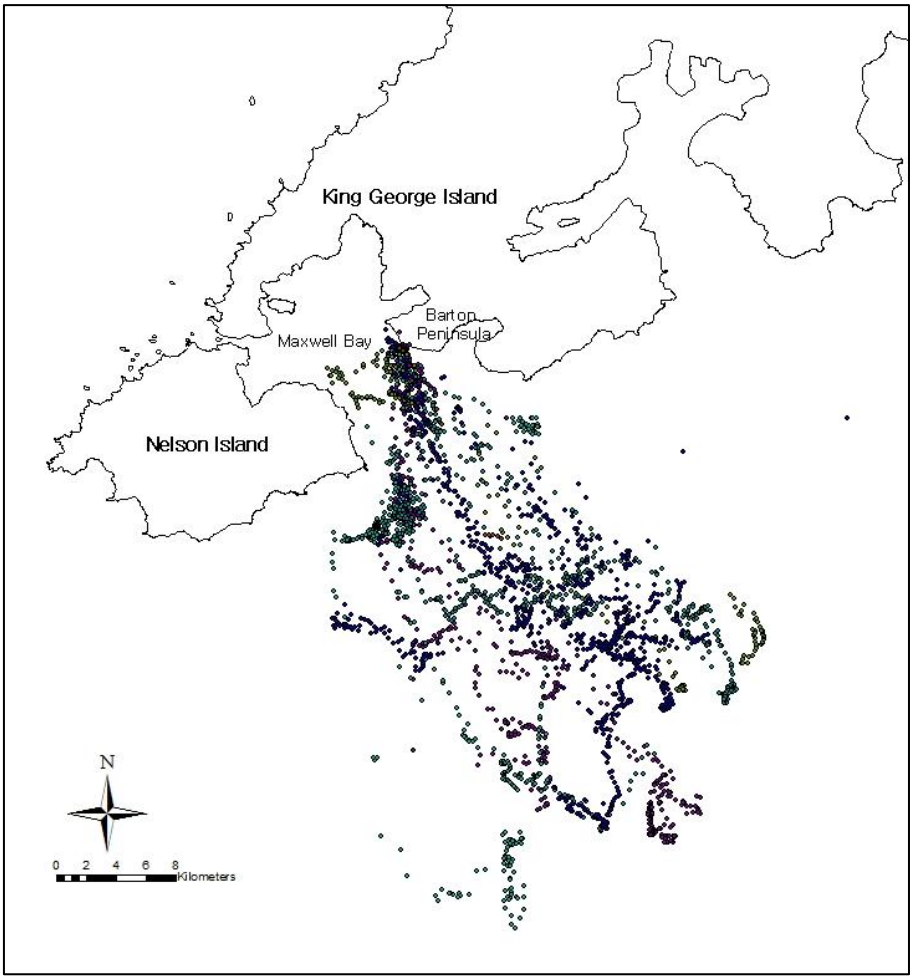


Figure 6. Foraging trips of female Chinstrap penguins (n = 6)

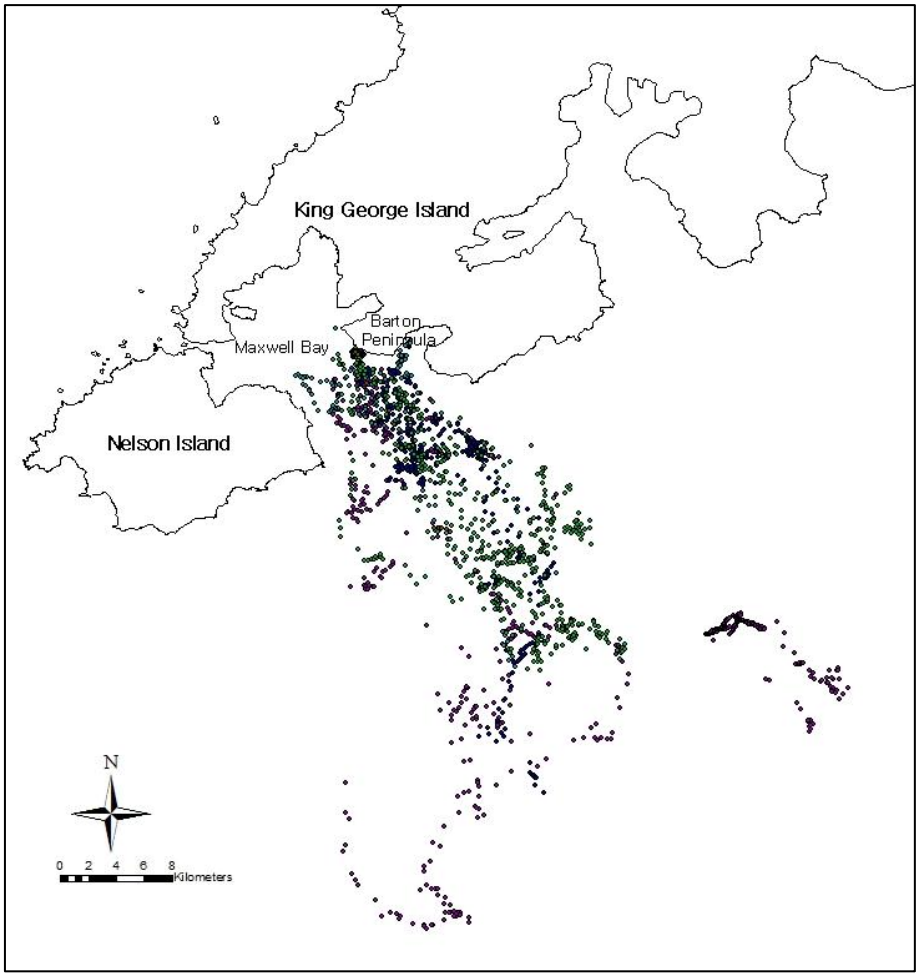


Figure 7. Foraging trips of male Chinstrap penguins (n = 4)

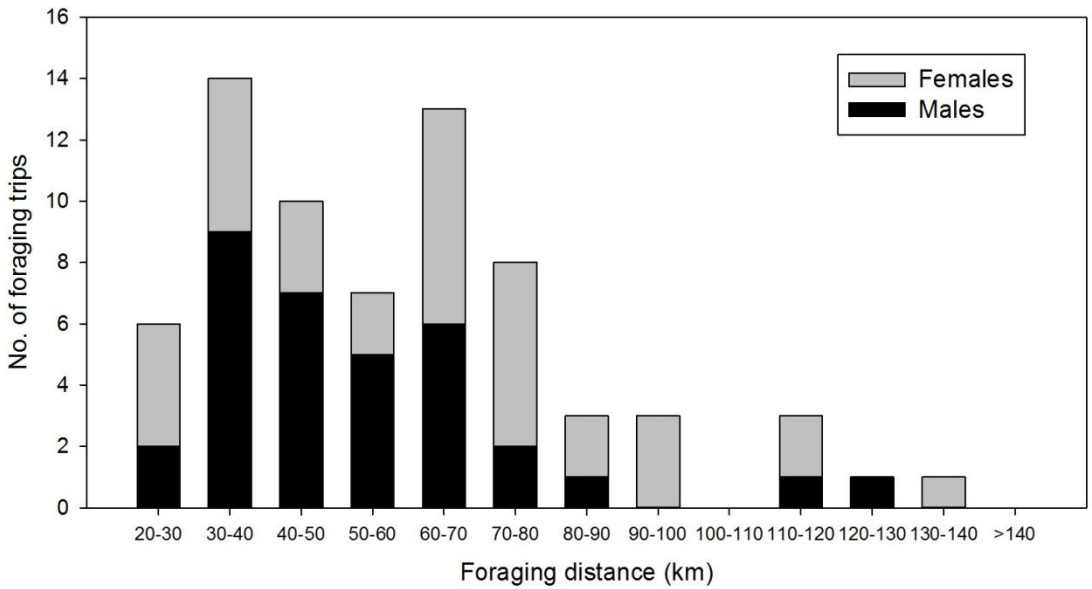


Figure 8. Foraging trips of Chinstrap penguins tracked by GPS loggers

Ⅴ. Discussion

1. Differences between species

According to the competitive exclusion principle, two species in a community cannot occupy the exact same niche, and competition between the species acts as a driving force for adaptation, resulting in occupying different niches (MacArthur 1958; Hardin 1960). Since Chinstrap and Gentoo penguins breed sympatrically, competition and specialization are expected on overlapping food resources in the study area.

From the stable isotope analysis, Gentoo penguins showed higher $\delta^{13}C$ value (−27.02±0.44 ‰) in their blood samples than Chinstrap penguins (−27.72±0.34 ‰). According to France (1995) and Cherel and Hobson (2007), the high $\delta^{13}C$ value of marine predator is generally derived from inshore food web, which is mainly based on benthic algae, while the low $\delta^{13}C$ value is closely related with offshore ecosystem. Hence, the result indicates that Gentoo penguins foraged in inshore areas, whereas Chinstrap penguins foraged in offshore areas, supporting the hypothesis about interspecific segregation in foraging areas. This spatial pattern was also shown in previous studies using GPS loggers to track foraging trips of two penguin species (Kokubun et al. 2010; Miller et al. 2010).

However, there was no sign of trophic level segregation indicated by $\delta^{15}N$ values of Chinstrap (7.65±0.42 ‰) and Gentoo penguins (7.73±0.47 ‰). Since $\delta^{15}N$ values of fish species are higher than krill (Polito et al. 2011), this result is in discord with previous studies using stomach content analysis, which indicates that Gentoo penguins catch larger krill or more fish than Chinstrap penguins (Kokubun et al. 2010; Miller et al. 2010). Polito et al. (2011) also estimated krill composition of the diet on Livingston Island to be 83.8 % and 89.4 % (in 2008, 2009) in Chinstrap penguin chicks and 69.1 %, 53.1 % (in 2008, 2009) in Gentoo penguin chicks. However, in this study, the estimated proportion of krill in the diet was almost the same in Chinstrap and Gentoo penguin chicks (79.2 % and 78.9 %, respectively).

Marine predators react to environmental changes depending on their foraging habits and the prey species that they use (Croxall et al. 1999). Compared to the previous study of Polito et al. (2011), diets of Gentoo penguins showed notably higher krill proportion, whereas diets of Chinstrap penguins maintained a similar level of krill proportion. The discordance seems derived from the variance of the prey abundance or distribution (Coria et al 2000; Rombolá et al. 2010) rather than from the regional differences since the previous studies were conducted in the South Shetland Islands, which is an adjacent area of the present study (Kokubun et al. 2010; Miller et al. 2010; Polito et al. 2011). Therefore, it is assumed that Gentoo penguins

responded more flexibly to the change of prey abundance or distribution than Chinstrap penguins. This assumption is also supported by the studies that show a greater annual variation in the diets of Gentoo penguins than for Chinstrap penguins (Coria et al 2000; Rombolá et al. 2010). The difference of flexibility of Chinstrap and Gentoo penguins can be partially explained concerning the distribution of the two species (Trivelpiece et al. 1987). Chinstrap penguins breed south of the Antarctic convergence, mostly on the Scotia Arc, where the Antarctic krill is a dominant prey species (Davis and Renner 2003). On the other hand, Gentoo penguins have a more extended distribution from the sub-Antarctic to Antarctic areas. Gentoo penguins have a broad range of prey composition throughout their extended habitats (Robinson and Hindell 1996; PuÈtz et al. 2001; Lescroel et al. 2004). Therefore, flexible foraging strategy of Gentoo penguins to prey availability would be beneficial considering the habitat range of this species (Miller et al. 2010)

2. Differences between sexes

Sexual size dimorphism is commonly reported in Pygoscelid penguins (e.g. Ainley and Emison 1972; Amat and Ferrer 1993; Polito et al. 2012). It affects the foraging behavior of males and females, reducing the level of intraspecific competition (Catry

et al. 2005). It is generally believed that the males are larger than the females in body size, especially in bill size, and that males may be better able to catch larger prey (Williams et al. 1992; Phillips et al. 2011). Besides the competition, more hostile nest defending behavior of male (Clarke et al. 1998) and sexual selection (Davis 1991) are also believed to be the cause of sexual size dimorphism (Davis and Renner 2003).

In this study, certain degrees of sexual size dimorphism in Chinstrap and Gentoo penguins were identified by morphological analysis. Males for both species were larger and heavier than females, and the difference in bill size appeared to be the most conspicuous. Several previous studies on penguins explained sexual size dimorphism in relation with the bigger prey size of males (Ainley and Emison 1972; Williams 1991; Forero 2002). This can be understood in the same context that the $\delta^{15}N$ values were higher in male Chinstrap (8.03±0.24 ‰) and Gentoo penguins (8.05±0.44 ‰) than in females of each species (7.56±0.40 and 7.65±0.30 ‰, respectively), indicating the higher trophic level of males, as the ^{15}N shows stepwise enrichment with increasing trophic level (DeNiro and Epstein 1981). This is also in accord with previous studies on various seabird species with sexual size dimorphism (Dehnhard et al. 2011; Michalik et al. 2013) and sexual segregation in foraging habits of Gentoo penguins (Bearhop et al. 2006), and a dietary study on Gentoo penguins (Williams et al. 1992).

On the other hand, there was no significant difference in $\delta^{13}C$ values between males (Chinstrap p.: −27.56±0.21 ‰, Gentoo p.: −26.87±0.58 ‰) and females (Chinstrap p.: −27.67±0.35 ‰, Gentoo p.: −26.99±0.25 ‰), indicating that their foraging range is not sexually separated, since the $\delta^{13}C$ value of marine predator is mainly affected by foraging area (Cherel and Hobson 2007). This is in accord with a previous study on sexual foraging specialization of Gentoo penguins (Bearhop et al. 2006). Some seabird species are intersexually segregated in their foraging area (Phillips et al. 2011). Among genus *Pygoscelis*, only the Adelie penguin showed that females on average traveled on longer foraging trips than males, ranging greater distances (Clarke et al. 1998). However, unlike the case of Adelie penguins, although the mean $\delta^{13}C$ value of females were slightly lower than the males in this study, the difference was not great enough to be statistically significant. The results of the GPS tracking of Chinstrap penguins also showed that there were no sexual differences in the foraging range. However, defining and excluding the short foraging trips from analysis was based on my discretion. Thus, further analysis of the foraging trip patterns would help to understand the foraging habits of male and female Chinstrap penguins.

Consequentially, intersexual diet variation of Chinstrap and Gentoo penguins appears predominantly related to the prey size and trophic level, rather than the geographical segregation.

3. Differences between ages

It is generally believed that the chicks have higher nutritional demands than adults for rapid growth in body size (Massias and Becker 1990; Starck and Ricklefs 1998), and that several Antarctic seabird species show selective provisioning of prey with good nutritional quality to their chicks. However, the $\delta^{15}N$ values were lower in the chicks of Chinstrap (7.32±0.18 ‰) and Gentoo penguins (7.34±0.55 ‰) in this study, than in adult males (8.03±0.24 and 8.05±0.44 ‰, respectively) and females (7.56±0.40 and 7.65±0.30 ‰, respectively), suggesting that the adults feed their chicks on smaller prey of a lower trophic level (DeNiro and Epstein 1981). According to the known trophic levels of the main prey species of Chinstrap and Gentoo penguins (Polito et al. 2011), the proportion of the krill in the chick diet is estimated higher than the adult diet (Table 10). Therefore, the hypothesis that adults feed their chicks on different prey from their own diet is accepted, but the aspect of selective provisioning is different from previous studies. As fish are generally known to be nutritionally better food than crustaceans including krill (Clarke and Prince 1980; Hislop et al. 1991; Anthony et al. 2000), the selectivity of prey items in provisioning of Chinstrap and Gentoo penguins may be the result of the abundance and the convenience of handling or carrying the prey for chicks, rather than the nutritional demands of the chicks.

Meanwhile, the $\delta^{13}C$ values were lower in chicks of Chinstrap (−28.08±0.18 ‰) and Gentoo penguins (−27.44±0.26 ‰), than in the adult males (−27.56±0.21 and −26.87±0.58 ‰, respectively) and females (−27.67±0.35 and −26.99±0.25 ‰, respectively), indicating that their diets originated from offshore areas (Cherel and Hobson 2007). This suggests that the adults make longer foraging trips on purpose to feed their chicks, and therefore, spend more energy to breed.

Ⅵ. Conclusions

The present study illustrated that Chinstrap and Gentoo penguins may reduce interspecific competition by the separation of foraging areas, rather than the selection of prey species. Differences of prey composition of Chinstrap and Gentoo penguins were not detected in this study, and it is supposed to be derived from the flexible response of Gentoo penguins to temporal variation of the abundance and distribution of prey species.

Clear sexual dimorphism appeared in both species. The male and female Chinstrap and Gentoo penguins consumed prey in different trophic levels. Evidence of intersexual segregation in foraging areas was not detected.

Prey of the lower trophic level, which are supposed to be mostly krill, appear to occupy a greater proportion in the diet of chicks, whereas adult penguins themselves relatively rely more on preys of a higher trophic level such as fish. Adult Chinstrap and Gentoo penguins seem to make longer foraging trips on purpose to catch prey for their chicks. The foraging trips are in a low trophic level, but highly available or easier to handle.

Ⅶ. References

Ainley, D. and W. Emison. 1972. Sexual size dimorphism in Adélie penguins. Ibis 114:267-271.

Ainley, D. G., G. Ballard, K. J. Barton, B. J. Karl, G. H. Rau, C. A. Ribic, and P. R. Wilson. 2003a. Spatial and temporal variation of diet within a presumed metapopulation of Adélie penguins. Condor 105:95-106.

Ainley, D. G., R. G. Ford, E. D. Brown, R. M. Suryan, and D. B. Irons. 2003b. Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. Ecology 84:709-723.

Amat, J. A., J. Viñuela, and M. Ferrer. 1993. Sexing Chinstrap Penguins (*Pygoscelis antarctica*) by morphological measurements. Colonial Waterbirds 16:213-215.

Anthony, J., D. Roby, and K. Turco. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. Journal of Experimental Marine Biology and Ecology 248:53-78.

Bearhop, S., S. Waldron, S. C. Votier, and R. W. Furness. 2002. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. Physiological and Biochemical Zoology 75:451-458.

Bearhop, S., R. A. Phillips, R. McGill, Y. Cherel, D. A. Dawson, and J. P. Croxall. 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. Marine Ecology Progress Series 311:157-164.

Brasso, R. L., S. Abel, and M. J. Polito. 2012. Pattern of mercury allocation into egg components is independent of dietary exposure in Gentoo penguins. Archives of Environmental Contamination and Toxicology 62:494-501.

Browne, T., C. Lalas, T. Mattern, and Y. Van Heezik. 2011. Chick starvation in yellow-eyed penguins: Evidence for poor diet quality and selective provisioning of chicks from conventional diet analysis and stable isotopes. Austral Ecology 36:99-108.

Catry, P., R. A. Phillips, and J. P. Croxall. 2005. Sexual segregation in birds: patterns, processes and implications for conservation. Sexual segregation in vertebrates: ecology of the two sexes, pp. 351-378, Cambridge University Press, Cambridge.

Cherel, Y., K. A. Hobson, and S. Hassani. 2005. Isotopic discrimination between food and blood and feathers of captive penguins: implications for dietary studies in the wild. Physiological and Biochemical Zoology 78:106-115.

Cherel, Y. and K. A. Hobson. 2007. Geographical variation in carbon stable isotope signatures of marine predators: a

tool to investigate their foraging areas in the Southern Ocean. Marine Ecology Progress Series 329:281–287.

Clarke, A. and P. A. Prince. 1980. Chemical composition and calorific value of food fed to mollymauk chicks *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. Ibis 122:488–494.

Clarke, J., B. Manly, K. Kerry, H. Gardner, E. Franchi, S. Corsolini, and S. Focardi. 1998. Sex differences in Adélie penguin foraging strategies. Polar Biology 20:248–258.

Coria, N., M. Libertelli, R. Casaux, and C. Darrieu. 2000. Inter-annual variation in the autumn diet of the gentoo penguin at Laurie Island, Antarctica. Waterbirds 23:511–517.

Croxall, J. and G. Lishman. 1987. The food and feeding ecology of penguins. In: Seabirds: feeding ecology and role in marine ecosystems (J. P. Croxall, ed.), pp. 101–133. Cambridge University Press, Cambridge.

Croxall, J. and P. Prince. 1980. The food of gentoo penguins *Pygoscelis papua* and macaroni penguins *Eudyptes chrysolophus* at South Georgia. Ibis 122:245–253.

Croxall, J. P. 1987. Seabirds: feeding ecology and role in marine ecosystems. Cambridge University Press, Cambridge.

Croxall, J., K. Reid, and P. Prince. 1999. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. Marine Ecology Progress Series 177:115–131.

Davis, L. 1991. Mate choice and sexual dimorphism in penguins. In: *Acta XX Congressus Internationalis Ornithologici* (Ed. by Bell, B. D., Cossee, R. O., Flux, J. E. C., Heather, B. D., Hitchmough, R. A., Robertson, C. J. R. and Williams, M. J.), pp. 1352-1360. New Zealand Ornithological Congress Trus Board, Wellington, New Zealand.

Davis, L. S. and M. Renner. 2003. Penguins. T & A D Poyser, London.

Dehnhard, N., C. C. Voigt, M. Poisbleau, L. Demongin, and P. Quillfeldt. 2011. Stable isotopes in southern rockhopper penguins: foraging areas and sexual differences in the non-breeding period. Polar Biology 34:1763-1773.

De Leon, A., J. Fargallo, and J. Moreno. 1998. Parental body size affects meal size in the chinstrap penguin (*Pygoscelis antarctica*). Polar biology 19:358-360.

Del Hoyo, J., A. Elliot, and J. Sargatal. 1992. Handbook of the Birds of the World. Lynx Editions, Barcelona.

DeNiro, M. J. and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:495-506.

DeNiro, M. J. and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45:341-351.

Deuel Jr., H. J. 1955. The lipids II. Biochemistry: Digestion, absorption, transport and storage.Interscience, New York.

Duffy, D. C. and S. Jackson. 1986. Diet studies of seabirds: a review of methods. Colonial Waterbirds 9:1-17.

Dunton, K. H. 2001. $\delta^{15}N$ and $\delta^{13}C$ measurements of Antarctic Peninsula fauna: trophic relationships and assimilation of benthic seaweeds. American Zoologist 41:99-112.

Forero, M. G., K. A. Hobson, G. R. Bortolotti, J. A. Donázar, M. Bertellotti, and G. Blanco. 2002. Food resource utilisation by Magellanic penguin evaluated through stable isotope analysis: segregation by sex and age and influence of offspring quality. Marine Ecology Progress Series 234:289-299.

Forero, M. G., J. González-Solís, K. A. Hobson, J. A. Donázar, M. Bertellotti, G. Blanco, and G. R. Bortolotti. 2005. Stable isotopes reveal trophic segregation by sex and age in the southern giant petrel in two different food webs. Marine Eology Progress Series 296:107-113.

France, R. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Marine Ecology Progress Series. 124:307-312.

Fry, B. 2006. Stable isotope ecology. Springer, New York.

Gales, N. and A. Cheal. 1992. Estimating diet composition of the Australian sea lion (*Neophoa cinerea*) from scat analysis: an unreliable technique. Wildlife Research 19:447-455.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292-1297.

Hauck, R. D., 1982. Nitrogen-isotope ratio analysis. In: Methods of Soil Analysis. Part 2: Chemical and Microbiological Properties. (Page, A.L., Miller, R.H., Keeney, D.R., eds.), pp. 735-779. American Society of Agronomy, Soil Science Society of America, Madison, Wisconsin.

Hislop, J., M. Harris, and J. Smith. 1991. Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. Journal of Zoology 224:501-517.

Hobson, K. and H. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using delta-13 C and delta-15 N analysis. Marine Ecology Progress Series 84:9-18.

Hobson, K. A. and R. G. Clark. 1992. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. Condor 94:189-197.

Hobson, K. A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Marine Ecology Progress Series 95:7-18

Hobson, K. A., J. F. Piatt, and J. Pitocchelli. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology:786-798.

Hodum, P. J. and K. A. Hobson. 2000. Trophic relationships among Antarctic fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from

stable-isotope (delta^{15}N and delta^{13}C) analyses. Marine Ecology Progress Series 198:273-281.

Iverson, S. J., A. M. Springer, and A. S. Kitaysky. 2007. Seabirds as indicators of food web structure and ecosystem variability: qualitative and quantitative diet analyses using fatty acids. Marine Ecology Progress Series 352:235-244.

Jackson, S. and P. G. Ryan. 1986. Differential digestion rates of prey by white-chinned petrels (*Procellaria aequinoctialis*). Auk 103:617-619.

Jackson, S., D. Duffy, and J. Jenkins. 1987. Gastric digestion in marine vertebrate predators: in vitro standards. Functional Ecology 1:287-291.

Kokubun, N., A. Takahashi, Y. Mori, S. Watanabe, and H.-C. Shin. 2010. Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. Marine Biology 157:811-825.

KOPRI and Ministry of Environment. 2009. Management plan for Antarctic specially protected area No. 171: Narebski Point, Barton Peninsula, King George Island. Korea Polar Research Institute and Ministry of Environment.

Lescroel, A., V. Ridoux, and C. A. Bost. 2004. Spatial and temporal variation in the diet of the gentoo penguin (*Pygoscelis papua*) at Kerguelen Islands. Polar Biology 27:206-216.

Lewis, S., T. Sherratt, K. Hamer, and S. Wanless. 2001. Evidence of intra-specific competition for food in a pelagic seabird. Nature 412:816-819.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599-619.

Massias, A. and P. H. Becker. 1990. Nutritive value of food and growth in Common Tern *Sterna hirundo* chicks. Ornis Scandinavica 21:187-194.

Michalik, A., R. A. McGill, H. J. van Noordwijk, J. F. Masello, R. W. Furness, T. Eggers, and P. Quillfeldt. 2013. Stable isotopes reveal variable foraging behaviour in a colony of the Imperial Shag *Phalacrocorax atriceps*: differences between ages, sexes and years. Journal of Ornithology 154:239-249.

Miller, A. K., M. A. Kappes, S. G. Trivelpiece, and W. Z. Trivelpiece. 2010. Foraging-niche separation of breeding gentoo and chinstrap penguins, South Shetland Islands, Antarctica. Condor 112:683-695.

Ministry of Environment. 2007. The fundamental study for designation of Antarctic Specially Protected Area. BSPN07030-71-3. Ministry of Environment.

Ministry of Environment. 2012. Research on management and monitoring of Antarctic specially protected area. BSPN11110-235-7. Ministry of Environment.

Mizutani, H. and E. Wada. 1988. Nitrogen and carbon isotope ratios in seabird rookeries and their ecological implications. Ecology:340-349.

Montevecchi, W. A. 1993. Birds as indicators of change in marine prey stocks. In: Birds as Monitors of Environmental Change (R. W. Furness and J. J. D. Greenwood, eds.), pp. 217-266. Chapman & Hall, London.

Montevecchi, W. A. and R. A. Myers. 1995. Prey harvests of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. Marine Ecology Progress Series 117:1-9.

Newman, S. H., A. Chmura, K. Converse, A. M. Kilpatrick, N. Patel, E. Lammers, and P. Daszak. 2007. Aquatic bird disease and mortality as an indicator of changing ecosystem health. Marine Ecology Progress Series 352:299-309.

Phillips, D. L. and J. W. Gregg. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127:171-179.

Phillips, D. L. and J. W. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261-269.

Phillips, R. A., R. A. McGill, D. A. Dawson, and S. Bearhop. 2011. Sexual segregation in distribution, diet and trophic level

of seabirds: insights from stable isotope analysis. Marine Biology 158:2199–2208.

Polito, M. J., W. Z. Trivelpiece, N. J. Karnovsky, E. Ng, W. P. Patterson, and S. D. Emslie. 2011. Integrating stomach content and stable isotope analyses to quantify the diets of pygoscelid penguins. Plos one 6:e26642.

Polito, M. J., G. V. Clucas, T. Hart, and W. Z. Trivelpiece. 2012. A simplified method of determining the sex of pygoscelis penguins using bill measurements. Marine Ornithology 40:89–94.

PuÈtz, K., R. J. Ingham, J. G. Smith, and J. P. Croxall. 2001. Population trends, breeding success and diet composition of gentoo Pygoscelis papua, magellanic Spheniscus magellanicus and rockhopper Eudyptes chrysocome penguins in the Falkland Islands. A review. Polar Biology 24:793–807.

Robinson, S. A. and M. A. Hindell. 1996. Foraging ecology of gentoo penguins Pygoscelis papua at Macquarie Island during the period of chick care. Ibis 138:722–731.

Rombolá, E. F., E. Marschoff, and N. Coria. 2010. Inter–annual variability in Chinstrap penguin diet at South Shetland and South Orkneys Islands. Polar Biology 33:799–806.

Selander, R.K. 1972. Sexual selection and dimorphism in birds. In: Sexual Selection and the Descent of Man (B. G. Campbell, ed.), pp. 180–230. Aldine, Chicago.

Starck, J. M. and R. E. Ricklefs. 1998. Avian growth and development: evolution within the altricial–precocial spectrum. Oxford University Press, Oxford.

Seppelt, R., T. Green, and B. Schroeter. 1995. Lichens and mosses from the Kar Plateau, Southern Victoria Land, Antarctica. New Zealand Journal of Botany 33:203–220.

Shirihai, H. 2002. A complete guide to Antarctic wildlife: The birds and marine mammals of the Antarctic continent and the southern ocean. A & C Black, London.

Stonehouse, B. 1970. Geographic variation in Gentoo penguins *Pygoscelis papua*. Ibis 112:52–57.

Storer, R. W. 1966. Sexual dimorphism and food habits in three North American accipiters. Auk 83:423–436.

Sydeman, W. J., K. A. Hobson, P. Pyle, and E. B. McLaren. 1997. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. Condor 99:327–336.

Thompson, D. R., K. Lilliendahl, J. Sólmundsson, R. W. Furness, S. Waldron, and R. A. Phillips. 1999. Trophic relationships among six species of Icelandic seabirds as determined through stable isotope analysis. Condor 101:898–903.

Tierney, M., C. Southwell, L. M. Emmerson, and M. A. Hindell. 2008. Evaluating and using stable–isotope analysis to infer diet composition and foraging ecology of Adélie

penguins *Pygoscelis adeliae*. Marine Ecology Progress Series 355:297−307.

Trivelpiece, W. Z., J. L. Bengtson, S. G. Trivelpiece, and N. J. Volkman. 1986. Foraging behavior of Gentoo and Chinstrap penguins as determined by new radiotelemetry techniques. Auk 103:777−781.

Trivelpiece, W. Z., S. G. Trivelpiece, and N. J. Volkman. 1987. Ecological segregation of Adelie, gentoo, and chinstrap penguins at King George Island, Antarctica. Ecology 68:351−361.

Volkman, N. J., P. Presler, and W. Trivelpiece. 1980. Diets of pygoscelid penguins at King George Island, Antarctica. Condor 82:373−378.

Warham, J. 1972. Breeding seasons and sexual dimorphism in Rockhopper Penguins. The Auk 89:86−105.

Williams, T. 1991. Foraging ecology and diet of gentoo penguins Pygoscelis papua at South Georgia during winter and an assessment of their winter prey consumption. Ibis 133:3−13.

Williams, T. D., A. Kato, J. P. Croxall, Y. Naito, D. R. Briggs, S. Rodwell, and T. R. Barton. 1992. Diving pattern and performance in nonbreeding gentoo penguins (*Pygoscelis papua*) during winter. Auk 109:223−234.

Williams, T. D. 1995. The penguins. Oxford University Press. Oxford.

Wilson, R. P., K. Putz, G. Peters, B. M. Culik, J. A. Scolaro, J. B. Charrassin, Y. Ropert-Coudert. 1997. Long-term attachment of transmitting and recording devices to penguins and other seabirds. Wildlife Society Bulletin 25: 101-106.

초 록

킹조지섬에 서식하는 젠투펭귄과 턱끈펭귄의 안정성 동위원소를 이용한 식이 습성 연구

잠수성 바닷새의 생태는 해양 생물자원의 분포 및 풍부도에 크게 영향을 받는다. 그러므로 각 종의 다양한 식이 습성을 밝히는 것은 환경 변화를 반영하는 지표종에 대한 이해 및 종의 관리와 보전에 있어 중요한 의미를 가진다. 본 연구에서는 킹조지섬에서 번식 중인 턱끈펭귄과 젠투펭귄의 혈중 안정성 동위원소 ^{13}C와 ^{15}N의 농도를 이용하여 종간, 성별간, 그리고 연령간 식이물의 영양 단계 및 기원의 차이를 중점적으로 연구하였다. 또한 성적 이형성에 따른 식이 습성 차이를 설명하기 위하여 성조 암컷과 수컷의 형태적인 차이를 분석하였으며, GPS추적장치를 이용하여 턱끈펭귄의 채이 지역을 조사하였다. 안정성 동위원소 분석을 위한 혈액 채취는 2013년 1월 13일에서 2월 6일 사이에 이루어졌으며, 이는 새끼들이 둥지에 머무는 시기 후반부터 보육원을 형성하기 시작하는 시기를 포함한다. 성조를 포획할 때는 혈액 채취와 동시에 날개 길이, 발 길이, 부리 길이, 부리 깊이, 머리 길이 및 무게를 측정하였다. 채이 지역 조사를 위한 GPS 추적장치는 총 5개를 두 차례에 걸쳐 턱끈펭귄 10마리에 부착하였다. 연구 결과 턱끈펭귄과 젠투펭귄의 먹이 영양 단계에는 차이가 없었으며, 턱끈펭귄은 외해에서, 젠투펭귄은 내해에서 먹이 활동을 하는 것을 확인하였다. 두 종 모두 수컷이 암컷보다 크기가 컸으며, 특히 부리 길이와

깊이에서 큰 차이를 보였다. 또한 두 종의 수컷은 암컷에 비해 높은 영양단계를 보였으나, 전반적인 채이 지역에 있어서는 뚜렷한 분리 현상을 보이지 않는 것으로 나타났다. 연령간 비교에서는 두 종 모두 새끼의 $\delta^{15}N$ 값이 성조보다 확연히 낮은 것으로 나타나 성조가 직접 섭취하는 식이물에 비해 새끼에게 더 영양단계가 낮은 먹이를 먹인다는 것과, 새끼의 $\delta^{13}C$ 값이 가장 낮은 것으로 보아 새끼에게는 성조의 먹이에 비해 더 먼 바다에서 사냥한 먹이를 급이하였다는 것을 확인하였다.

주요어: 성적 이형성, 식이 습성, 안정성 동위원소, 젠투펭귄, 킹조지섬, 턱끈펭귄

학 번: 2011-23499