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CHANGES IN STABLE CARBON AND NITROGEN ISOTOPE RATIOS IN SOOTY AND SHORT-TAILED SHEARWATERS DURING THEIR NORTHWARD MIGRATION[1]

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Abstract. Migratory behaviors and associated food habits were investigated for two closely-related seabird species, Sooty (*Puffinus griseus*) and Short-tailed Shearwaters (*P. tenuirostris*), sampled in the western North Pacific from April to June in 1986, 1989, and 1990 using their carbon and nitrogen isotope ratios (muscle $\delta^{13}C$ and $\delta^{15}N$). The shearwaters exhibited $\delta^{13}C$ and $\delta^{15}N$ values of −24.5 to −17.6‰, and 7.3 to 13.0‰, respectively. Shearwaters showed areal differences in their stable isotope ratios: those from the oceanic group in June had significantly higher $\delta^{13}C$ and $\delta^{15}N$ values than those from the coastal area of northern Japan in April and May. The isotope compositions of both species increased along with their migration from the Southern Hemisphere to the North Pacific. The low stable isotope ratios in the birds from the coastal area strongly demonstrated the preservation of isotope ratios of prey in the Southern Hemisphere before their northward migration.

Significant differences in a $\delta^{13}C$–$\delta^{15}N$ map were also observed between two species as well as within single species in time and space. In the coastal area of northern Japan, Sooty Shearwaters showed somewhat higher $\delta^{13}C$ and $\delta^{15}N$ values than Short-tailed Shearwaters. However, no interspecific difference of their $\delta^{15}N$ value was found in the oceanic area of North Pacific, but the $\delta^{13}C$ value of Sooty Shearwater was significantly higher than these of Short-tailed Shearwater. The interspecific difference in the coastal and oceanic areas reflects their changing dietary difference.

Key words: Puffinus griseus; Puffinus tenuirostris; *stable isotope; carbon 13; nitrogen 15; trophic level; migration.*

INTRODUCTION

Stable isotope analyses of consumer and prey tissues represent a valuable method to assess trophic relationships in marine and terrestrial ecosystems (DeNiro and Epstein 1978, Wada et al. 1987, Fry 1988, Hobson and Welch 1992). Nitrogen isotope ratios ($\delta^{15}N$) of animals reflect the trophic levels within food chains, increasing of about 3 to 4‰ per trophic level (DeNiro and Epstein 1981, Minagawa and Wada 1984). Though stable isotope analysis has been used to determine trophic relationships and diets of birds (Hobson 1987, 1990, 1991, 1993; Mizutani et al. 1990; Hobson et al. 1994), no studies have demonstrated changes in stable isotope signatures of birds during migration when diets or background isotope signatures of prey can change regionally.

Sooty (*Puffinus griseus*) and Short-tailed Shearwaters (*P. tenuirostris*) are closely related species that breed in the Southern Hemisphere from September to April and then migrate to the Northern Hemisphere during the northern summer. Both shearwaters dominate the avifauna in summer in the subarctic North Pacific. The Sooty Shearwater is distributed in the oceanic waters of 40°–55°N in the North Pacific in summer (Ogi et al. 1981, Guzman and Myres 1983, Ogi 1984, Briggs and Chu 1986), whereas the Short-tailed Shearwater predominates in the waters of 45°–60°N in the North Pacific and adjacent sea areas

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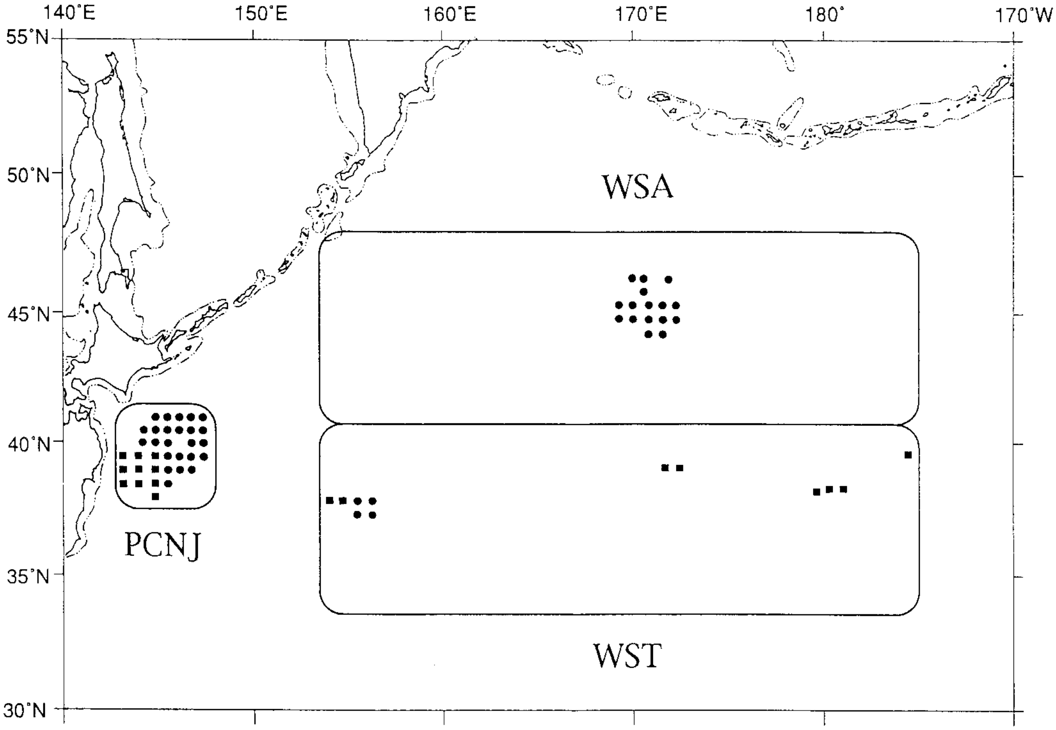

FIGURE 1. Sampling locations for Sooty (■) and Short-tailed (●) Shearwaters in the North Pacific in 1986, 1989 and 1990. PCNJ: Pacific coast of northern Japan in April and May, WST: western subtropical Pacific in June, WSA: western subarctic Pacific in June.

(Shuntov 1972, Ogi et al. 1980, Harrison 1983, Ogi 1984). Sooty Shearwater feeds mainly on abundant planktivorous fish and squid (Sanger 1983, Ogi 1984, Shiomi and Ogi 1992), while Short-tailed Shearwater depends upon zooplankton in addition to fish and squid (Ogi et al. 1980, Sanger 1983, Skira 1986).

In this study, we measured the stable carbon and nitrogen isotope ratios of muscle tissues of the two shearwater species to assess evidence for their dietary changes during their northward migration. We also examined the ecological segregation in trophic relationships and diets between the two closely-related species by the stable isotope analysis.

MATERIALS AND METHODS

The birds sampled in this study were incidentally entangled in gill nets set for salmon and squid in the western North Pacific from April to June in 1986, 1989, and 1990. Pectoral muscle tissues of 18 Sooty and 44 Short-tailed Shearwaters were used for stable isotope analyses. The sampling stations were grouped into three areas based on sampling months and physicocheminal and biological oceanographic structures (Ogi 1984, Sanger and Ainley 1988): Pacific coast of northern Japan in April and May (PCNJ), western subtropical Pacific in June (WST), western subarctic Pacific in June (WSA) (Fig. 1). In addition, $\delta^{13}C$ and $\delta^{15}N$ were measured for *Euphausia pacifica, Engraulis japonicus* and *Cololabis saira* sampled from the northwestern Pacific and *Balaenoptera acutorostrata* from the Antarctic.

Muscle tissues from these birds were ground to fine powders and lipid extracted using a chloroform : methanol (2:1) solution. The following analytical procedures for carbon and nitrogen isotope ratios were the same as those reported by Minagawa et al. (1984). Approximately 10–20 mg of the powdered muscle was put into a quartz tube containing 1 g of CuO, 0.5 g Cu metal and a piece of silver foil. The tube was then evacuated and sealed. The tube was preheated at 500°C for 30 min and combusted at 850°C for 2 hr. After cooling, CO_2 and N_2 were separated cryogenically

TABLE 1. $\delta^{13}C$ and $\delta^{15}N$ values of Sooty and Short-tailed Shearwaters.

	Sooty Shearwater				Short-tailed Shearwater				
Sample group†	*n*	Mean	SD	Range	*n*	Mean	SD	Range	t-test (*P*)
$\delta^{13}C$ (‰)									
PCNJ	10	−20.1	0.63	−21.2 to −19.2	24	−23.0	0.87	−24.5 to −20.5	***
WST	8	−18.5	0.76	−19.7 to −17.6	4	−19.7	0.29	−19.9 to −19.4	*
WSA					16	−20.1	0.70	−22.0 to −19.0	
$\delta^{15}N$ (‰)									
PCNJ	10	9.2	0.72	8.2 to 10.0	24	8.0	0.46	7.3 to 8.8	***
WST	8	10.9	1.36	8.4 to 13.0	4	11.6	0.46	11.1 to 12.2	n.s.
WSA					16	11.4	0.62	9.5 to 12.1	

n.s. = no significant difference, * = $0.01 < P < 0.05$, *** = $P < 0.001$.
† See Figure 1.

with liquid nitrogen and a dry ice-ethanol mixture. Carbon and nitrogen isotope ratios were measured by a Finnigan MAT 251 mass spectrometer fitted with a dual inlet and triple collector system. Isotope ratios were expressed as deviation from a standard as defined by the following equation:

$$\delta^{13}C, \delta^{15}N = \{R(\text{sample})/R(\text{standard}) - 1\} \cdot 1000\ (‰),$$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$.

Belemnite and atmospheric nitrogen were used as the carbon and nitrogen isotope standards, respectively. Calcium or sodium carbonate for $\delta^{13}C$ and a high-purity nitrogen gas for $\delta^{15}N$ were also used as working standards during isotope measurements. Standard deviations for stable isotope measurements were less than 0.1‰ for carbon and 0.2‰ for nitrogen.

RESULTS

AREAL DIFFERENCES

There were no differences of $\delta^{13}C$ and $\delta^{15}N$ values in Sooty and Short-tailed Shearwaters along with changes of their body mass and sex (Appendixes 1 and 2). Stable isotope analysis was thus performed without any distinction of body mass and sexual differences.

Significant differences in $\delta^{13}C$ and $\delta^{15}N$ values were clearly observed for Sooty and Short-tailed Shearwaters between the Pacific coast of northern Japan and the western subtropical Pacific (Table 1). Differences in *t*-test were as follows: Sooty Shearwater—$\delta^{13}C$ $t = 4.820$, df = 16, $P < 0.001$, $\delta^{15}N$ $t = 3.333$, df = 16, $P < 0.01$; Short-tailed Shearwater—$\delta^{13}C$ $t = 7.497$, df = 26, $P < 0.001$, $\delta^{15}N$ $t = 14.012$, df = 26, $P < 0.001$. Short-tailed Shearwater in the western subarctic Pacific in June also exhibited significantly higher $\delta^{13}C$ and $\delta^{15}N$ values than those of the birds in the Pacific coast of northern Japan in April and May ($\delta^{13}C$ $t = 9.474$, df = 38, $P < 0.001$, *t*-test; $\delta^{15}N$ $t = 16.511$, df = 38, $P < 0.001$, *t*-test). The $\delta^{13}C$ and $\delta^{15}N$ of the two shearwaters clearly increased along with their migration from Pacific coast of northern Japan in April and May to western subtropical and subarctic areas in June.

TROPHIC RELATIONSHIPS

The isotopic compositions were also variable between two closely-related species (Table 1). In the Pacific coast of northern Japan, the Sooty Shearwater was enriched in heavier isotopes as compared to Short-tailed Shearwater ($\delta^{13}C$ $t = 9.017$, df = 32, $P < 0.001$, *t*-test; $\delta^{15}N$ $t = 5.097$, df = 32, $P < 0.001$, *t*-test) (Table 1). The differences of isotope ratios between the two species averaged 2.9‰ for carbon and 1.2‰ for nitrogen.

The difference in $\delta^{13}C$ between the two shearwaters was still significant in both the western subtropic (1.2‰, $t = 2.797$, df = 10, $P < 0.05$, *t*-test) and subarctic (1.6‰, $t = 4.906$, df = 22, $P < 0.001$, *t*-test). The $\delta^{15}N$ values showed wide range of overlap between the two species (western subtropic $t = 1.050$, df = 10, $P > 0.05$, *t*-test; western subarctic $t = 1.102$, df = 22, $P > 0.05$, *t*-test) (Table 1).

DISCUSSION

AREAL DIFFERENCES

Several factors can influence the isotopic differences in consumers in different marine areas. These include differences in isotopic signature of food webs due to oceanographic factors (Saino and Hattori 1987, Liu and Kaplan 1989), differences in prey selection, and differences in nutritional condition of birds (Hobson et al. 1993).

To assess the influence of differences in isotopic signature of food webs due to oceanographic factors, $\delta^{13}C$ and $\delta^{15}N$ values of primary producers, diets of the two shearwaters, and the other marine organisms in the oceanic areas relating to their migration course are shown in Table 2. The differences in $\delta^{13}C$ and $\delta^{15}N$ of marine organisms between the Pacific coast and the western subtropic are hardly discernible. Marine organisms in the western subarctic are somewhat low in isotopic values as compared to those in both the Pacific coast and the western subtropic. Based upon stable isotope values of marine organisms in the oceanic areas in question, the differences in $\delta^{13}C$ and $\delta^{15}N$ of Sooty and Short-tailed Shearwaters between the Pacific coast and the western subtropic should not be caused by differences in isotopic signature of their food base in the northwestern pacific.

Based upon the stomach contents, the predominant diet of Sooty Shearwater is fish, the wet mass percentage of which was 98.8% in the Pacific coast of northern Japan in April and May (Shiomi and Ogi 1992). While in the western subtropical Pacific in June and July fish (51.4%), squid (30.9%) and barnacles (15.2%) are the main diets. Therefore, isotopic values of the two shearwaters may differ between the Pacific coast and the western subtropic because of differences in prey selection.

The effect on the isotope ratios of differences in nutritional conditions of these birds is unknown. However, low $\delta^{13}C$ and $\delta^{15}N$ values of Sooty and Short-tailed Shearwaters in the Pacific coast in this study are somewhat different from predictable isotope values of these species when these species feed on fish with high $\delta^{13}C$ and $\delta^{15}N$ values in the Pacific coast. Low isotopic values of the two shearwaters in the Pacific coast cannot be sufficiently explained by the influence of differences in isotopic signature of food webs due to oceanographic factors and differences in their prey selection.

Both species in this study were in northward migration (Watabe et al. 1987). These species had just have arrived in the Northern Hemisphere in April and May. Therefore, low $\delta^{13}C$ and $\delta^{15}N$ values of Sooty and Short-tailed Shearwaters in the Pacific coast of northern Japan may be mainly caused by diet-isotope value lags due to turnover rates of the stable isotopes in muscle protein. In laboratory studies of turnover rates of the stable isotopes, the half-life of carbon in muscle tissue of gerbils (*Meriones unguiculatus*) was 27.6 days (Tieszen et al. 1983), and 12.4 days for Japanese Quail (*Coturnix japonica*) (Hobson and Clark 1992b). Though the turnover rates of carbon and nitrogen in muscle tissues in wild birds are unknown, these would probably have a half-life of few weeks due to high metabolic rates compared to captive birds.

In the Antarctic Ocean, the breeding area of the two shearwaters, the $\delta^{15}N$ values of fish available to these species are probably about 5–7‰, because the $\delta^{15}N$ values of POM and herbivorous animals (*Euphausuacea*) are 0.4–0.5‰ and 2.7–3.1‰, respectively (Table 2). On the other hand, the $\delta^{15}N$ values of marine food web components available to shearwaters in the northwestern Pacific are 5.4‰ for particulate organic matter (POM), 7.4‰ for *Eupausia pacifica* and 8.9–9.2‰ for fish, respectively (Table 2). Both the $\delta^{13}C$ and $\delta^{15}N$ values of the marine organisms in the Antarctic are significantly lower than those of corresponding organisms in the northwestern Pacific (Table 2). As reported by Wada et al. (1987), the ^{15}N and ^{13}C contents of POM and net plankton were quite low in comparison to those of temperate regions.

Consequently, low $\delta^{13}C$ and $\delta^{15}N$ values of Sooty and Short-tailed Shearwaters in the Pacific coast of northern Japan in April and May may be caused by the transient effects of diets consumed in the Southern Hemisphere before northward migration (Fig. 2). Alternatively, high $\delta^{13}C$ and $\delta^{15}N$ values of Sooty and Short-tailed Shearwaters in the western subtropical and subarctic Pacific in June suggested that both species had enough time to turnover their tissue and change their isotope ratios by feeding prey such as Euphausiid and Pacific saury (*Cololabis saira*) in the Northern Hemisphere during their northward migration until June (Fig. 2).

Analyzing the areal differences of the muscle $\delta^{15}N$ of Sooty Shearwater between the western and eastern parts of the North Pacific, for example, Minami (1992) determined that Sooty Shearwaters found in the North Pacific had been born in two areas, New Zealand and the southern South America. Differences in $\delta^{15}N$ content reflected the extremely high $\delta^{15}N$ of POM in the denitrifying zones of the eastern Pacific (Saino and Hattori 1987, Liu and Kaplan 1989). Therefore, the isotopic analyses of the

TABLE 2. $\delta^{13}C$ and $\delta^{15}N$ values of marine food-web components in the Antarctic and the western North Pacific.

Samples (*n*)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Location	Source
Antarctic Ocean				
Particulate organic matter	−27.4	0.53	61°26′S, 150°05′E	Wada et al. (1987)
	−26.4	0.37	60°00′S, 116°02′E	Wada et al. (1987)
Euphausia				
Euphausia triacantha	−29.1	3.1	61°32′S, 150°26′E	Wada et al. (1987)
Euphausia superba	−29.3	2.7	65°03′S, 118°03′E	Wada et al. (1987)
Whale				
Balaenoptera acutorostrata (18)	−24.0 ± 0.97	6.0 ± 0.60	58°–66°S, 138°E–170°W	This study
Pacific coast of northern Japan				
Particulate organic matter	—	5.4	39°59′N, 138°05′E	Sugisaki et al. (1991)
	−20.3	—	41°00′N, 142°20′E	Sugisaki (1989)
Euphausia				
Euphausia pacifica	−18.4	7.4	39°30′N, 147°47′E	This study
Western subtropical Pacific				
Fish				
Engraulis japonicus (1)	−18.7	8.9	41°00′N, 155°00′E	This study
Cololabis saira (15)	−18.5 ± 0.58	9.2 ± 0.58	39°22′N, 155°04′E	This study
Western subarctic Pacific				
Net plankton				
Calanoida	—	3.2, 3.5	50°00′N, 155°00′E	Wada and Hattori (1976)
Calanus cristatus	—	5.1	50°00′N, 155°00′E	Wada and Hattori (1976)

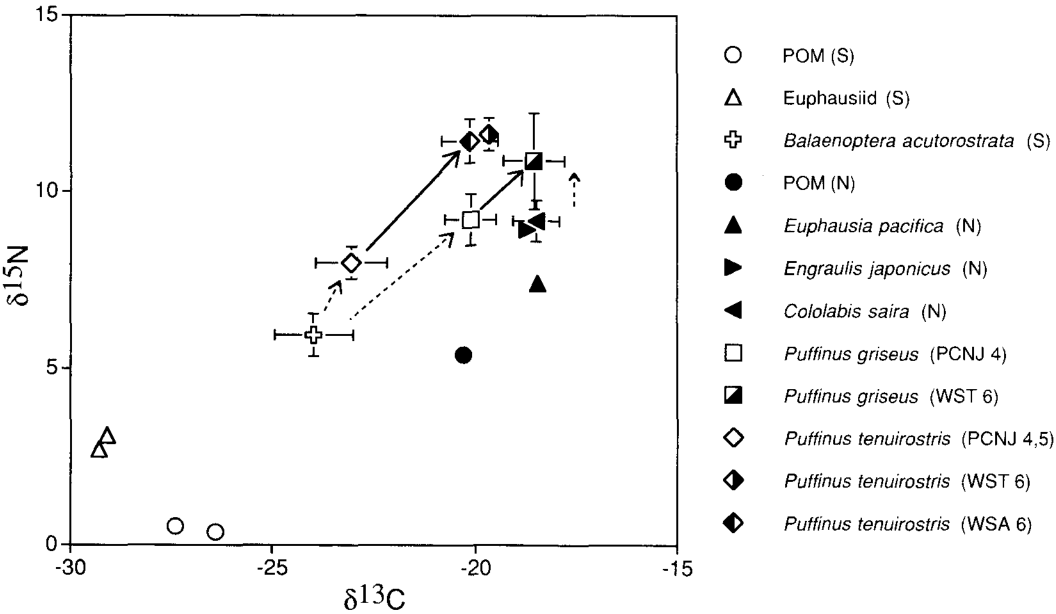

FIGURE 2. $\delta^{13}C$ and $\delta^{15}N$ values (Mean ± SD‰) of marine food web components in the Antarctic and the northwestern Pacific. Abbreviations in parentheses indicate locations and months (S: Antarctic Ocean; N: northwestern Pacific Ocean; PCNJ, WST, WSA: see Figure 1; 4, 5, 6: month). $\delta^{13}C$ and $\delta^{15}N$ values of POM(S) and Euphausiid(S) from Wada et al. (1987), and those of POM(N) from Sugisaki (1989) and Sugisaki et al. (1991).

migratory seabirds in time and space can provide useful information on their migratory mechanisms. In addition, isotopic analyses of tissues of short turnover rates such as liver and blood (Hobson and Clark 1992b, 1993) may be useful for the elucidation of food habits in short-term periods.

TROPHIC RELATIONSHIPS

Both species migrate trans-equatorially to the Northern Hemisphere during the non-breeding season. Since the two species occur in the same area during their migration, it is possible to analyze their dietary preferences based on their carbon and nitrogen isotope ratios.

Predominant prey species for Sooty Shearwater is the Japanese sardine (*Sardinops melanosticta*) and Pacific saury (*Cololabis saira*) in the western North Pacific (Ogi 1984, Shiomi and Ogi 1992). Other prey are squid (*Berryteuthis anonychus*), pelagic barnacle (*Lepas fascicularis*), and jellyfish (*Vellela lata*) (Shiomi and Ogi 1992). Although prey for the Sooty Shearwater in the breeding area is unknown, it perhaps feeds mainly on fish at the same trophic level as those in the North Pacific. Alternatively, the diet for Short-tailed Shearwater varies according to sea area in the western North Pacific (Ogi et al. 1980). It consists mainly of small-sized organisms such as larval and juvenile fish (*Pleurogrammus monopterigius*) and squid (Gonatidae), euphausiids (*Thysanoessa longipes*), amphipods (*Parathemisto*), copepods (*Calanus cristatus*), shrimp, and Thecosomata, all of which are usually abundant in the surface layer of the pelagic environment (Ogi et al. 1980). In the breeding area, Tasmania, the main food items of Short-tailed Shearwater are the euphausiid (*Nyctiphanes australis*), and arrow squid (*Notodarus sloani gouldi*), together with fish, other crustaceans, and squids forming a minor part of the diet (Skira 1986). Thus, the Short-tailed Shearwater depends upon zooplankton of lower trophic levels besides fish and squid compared to the Sooty Shearwater.

The $\delta^{15}N$ of animals in the marine food web increase about 3 to 4‰ per trophic level (Minagawa and Wada 1984, Wada et al. 1987, Fry 1988, Hobson and Welch 1992). However, Mizutani et al. (1991) and Hobson and Clark (1992a) estimated the $\delta^{15}N$ enrichment values of 2.4‰ and 1.4‰ for muscle of captive birds, Common Cormorant (*Phalacrocorax carbo*) and Ring-billed

Gull (*Larus delawarensis*), respectively. The ^{15}N enrichments in the muscle tissue-diet of piscivorous birds are less than those of the other marine organisms (Hobson and Welch 1992), while $\delta^{13}C$ of animals and birds increase slightly about 1‰ per trophic level and very close to those of their diet. Its $\delta^{13}C$ abundance thus shows those of available food source (Fry 1988, Hobson and Welch 1992).

Near the Pacific coast of northern Japan, the Sooty Shearwater had significantly higher $\delta^{15}N$ value than Short-tailed Shearwater with the difference of 1.2‰, suggesting that the trophic level of the Sooty Shearwater was high as compared to Short-tailed Shearwater. If their food habits are not so different between the Southern and Northern Hemispheres, the Sooty Shearwater may feed on prey organisms of higher trophic levels such as fish, while the Short-tailed Shearwater may feed, at least partially, on zooplankton as described above.

In the western subtropical Pacific, no difference in trophic level between the diets of the two species would exist. However, there must be the difference in food source between the two species, as suggested by the higher $\delta^{13}C$ of Sooty Shearwater. The Sooty Shearwater ($\delta^{13}C$: −18.5‰, $\delta^{15}N$: 10.9‰) sampled from the western subtropic may feed on mainly fish such as Pacific saury ($\delta^{13}C$: −18.5‰, $\delta^{15}N$: 9.2‰), while the Short-tailed Shearwater sampled from both the western subtropic and subarctic may feed on another prey organisms at the same trophic position with different $\delta^{13}C$ value as suggested by their stomach contents (Ogi et al. 1980, Ogi 1984, Skira 1986, Shiomi and Ogi 1992). Consequently, analyses of trophic relationships of the two shearwaters using stable isotope technique agreed well with previous studies analyzing their stomach contents.

CONCLUSIONS

The muscle $\delta^{13}C$ and $\delta^{15}N$ of the two migratory seabirds were variable depending upon the oceanographic factors through their prey organisms. Our results indicated that the trophic relationships of these seabirds could be elucidated by taking the seasonal and areal variations of their prey into consideration. More detailed information of feeding ecology in seabird species could be obtained by simultaneous measurements of stable isotopes and stomach contents. The stable isotope technique would thus provide more time integrated and quantitative information on food habits and migratory mechanisms of these seabird species for which detailed observations are quite difficult in the open ocean.

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LITERATURE CITED

Briggs, K. T., and E. W. Chu. 1986. Sooty Shearwaters off California: distribution, abundance and habitat use. Condor 88:355–364.

DeNiro, M. J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochim. Cosmochim. Acta 42:495–506.

DeNiro, M. J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochim. Cosmochim. Acta 45:341–351.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnol. Oceanogr. 35:1182–1190.

Guzman, J. R., and M. T. Myres. 1983. The occurrence of shearwaters (*Puffinus* spp.) off the west coast of Canada. Can. J. Zool. 61:2064–2077.

Harrison, P. 1983. Seabirds: an identification guide. Houghton Mifflin, Boston.

Hobson, K. A. 1987. Use of stable-carbon isotope analysis to estimate marine and terrestrial protein content in gull diet. Can. J. Zool. 65:1210–1213.

Hobson, K. A. 1990. Stable isotope analysis of Marbled Murrelets: evidence for freshwater feeding and determination of trophic level. Condor 92:897–903.

Hobson, K. A. 1991. Stable-isotopic determinations of the trophic relationships of seabirds: preliminary investigations of alcids from coastal British Columbia, p. 16–20. *In* W. A. Montevecchi and A. J. Gaston [eds.], Studies aspects of seabird feeding ecology. Can. Wildl. Serv. Occ. Pap. No. 68, Ottawa.

Hobson, K. A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Mar. Ecol. Prog. Ser. 95:7–18.

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

Hobson, K. A., and R. G. Clark. 1992b. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. Condor 94:179–186.

Hobson, K. A., and R. G. Clark. 1993. Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. Auk 110:638–641.

HOBSON, K. A., AND H. E. WELCH. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar. Ecol. Prog. Ser. 84:9–18.

HOBSON, K. A., R. T. ALISAUSKAS, AND R. G. CLARK. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. Condor 95:388–394.

HOBSON, K. A., J. F. PIATT, AND J. PITOCCHELLI. 1994. Using stable isotopes to determine seabird trophic relationships. J. Anim. Ecol. 63:786–798.

LIU, K.-K., AND I. R. KAPLAN. 1989. The eastern tropical Pacific as a source of ^{15}N-enriched nitrate in seawater off southern California. Limnol. Oceanogr. 34:820–830.

MINAGAWA, M., AND E. WADA. 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between ^{15}N and animal age. Geochim. Cosmochim. Acta 48:1135–1140.

MINAGAWA, M., D. A. WINTER, AND I. R. KAPLAN. 1984. Comparison of Kjeldahl and Combustion methods for measurement of nitrogen isotope ratios in organic matter. Anal. Chem. 56:1859–1861.

MINAMI, H. 1992. Relation between feeding ecology and $\delta^{13}C$, $\delta^{15}N$ values of Sooty (*Puffinus griseus*) and Short-tailed (*P. tenuirostris*) Shearwaters during their northward migration. M.Sc.thesis, Hokkaido Univ., Hakodate. (In Japanese)

MIZUTANI, H., M. FUKUDA, Y. KABAYA, AND E. WADA. 1990. Stable-carbon isotope ratios of feathers reveals feeding behavior of cormorants. Auk 107: 400–403.

MIZUTANI, H., Y. KABAYA, AND E. WADA. 1991. Nitrogen and carbon isotope compositions relate linearly in cormorant tissues and its diet. Isotopenpraxis 27:166–168.

OGI, H. 1984. Feeding ecology of the Sooty Shearwater in the western subarctic North Pacific Ocean, p. 78–84. *In* D. N. Nettleship, G. A. Sanger, and P. F. Springer [eds.], Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

OGI, H., T. KUBODERA, AND K. NAKAMURA. 1980. The pelagic feeding ecology of the Short-tailed Shearwater *Puffinus tenuirostris* in the subarctic Pacific region. J. Yamasina Inst. Ornith. 12:157–182.

OGI, H., K. SHIMAZAKI, AND K. NAKAMURA. 1981. Sooty Shearwaters in the subarctic North Pacific: Seasonal changes in body weight and molt. Res. Inst. North Pac. Fish. Hokkaido Univ. Spec. Vol., 207–215.

SAINO, T., AND A. HATTORI. 1987. Geographical variation of the water column distribution of suspended particulate organic nitrogen and its ^{15}N natural abundance in the Pacific and its marginal seas. Deep-Sea Res. 34:807–827.

SANGER, G. A. 1983. Diets and food web relationships of seabirds in the Gulf of Alaska and adjacent marine regions. Research Migratory Bird Section. Alaska, Proc. Rept., 91 p. (Final report to OCSEAP, U.S. Fish and Wildl. Serv.)

SANGER, G. A., AND D. G. AINLEY. 1988. Review of the distribution and feeding ecology of seabirds in the oceanic subarctic North Pacific Ocean. Bull. Ocean Res. Inst. Tokyo Univ. 26:161–186.

SHIOMI, K., AND H. OGI. 1992. Feeding ecology and body size dependence in diet of the Sooty Shearwater, *Puffinus griseus,* in the North Pacific. Proc. NIPR Symp. Polar biol. 5:105–113.

SHUNTOV, V. P. 1972. Sea birds and biological structure of the ocean (Translated from Russian). Nat. Tech. Inform. Serv., U.S. Dept. Comm. 1974.

SKIRA, I. J. 1986. Food of the Short-tailed Shearwater, *Puffinus tenuirostris,* in Tasmania. Aust. Wildl. Res. 13:481–488.

SUGISAKI, H. 1989. Ecology of the pelagic amphipod *Themisto japonica* in the Oyashio region and the Sea of Japan. Ph.D.diss. Tokyo Univ., Tokyo. (In Japanese)

SUGISAKI, H., M. TERAZAKI, E. WADA, AND T. NEMOTO. 1991. Feeding habits of a pelagic amphipod, *Themisto japonica.* Mar. Biol. 109:241–244.

TIESZEN, L. L., T. W. BOUTTON, K. G. TESDAHL, AND N. A. SLADE. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}C$ analysis of diet. Oecologia 57: 32–37.

WADA, E., AND A. HATTORI. 1976. Natural abundance of ^{15}N in particulate organic matter in the North Pacific Ocean. Geochim. Cosmochim. Acta 40:249–251.

WADA, E., M. TERAZAKI, Y. KABAYA, AND T. NEMOTO. 1987. ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on biogeochemical structure of the food web. Deep-Sea Res. 34:829–841.

WATABE, Y., N. OKA, AND N. MARUYAMA. 1987. Seasonal appearances of Short-tailed (*Puffinus tenuirostris*) and Sooty (*Puffinus griseus*) Shearwaters on the Tokyo-Kushiro line, Japan. J. Yamashina Inst. Ornith. 19:117–124.

APPENDIX 1. The sampling dates, sampling locations, measurements of body and $\delta^{13}C$, $\delta^{15}N$ values for Sooty Shearwaters.

Sample code	Date	Location	Sex	Body weight (g)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
		Pacific coast of northern Japan in April				
¥6674	1986 4 27	39°30′N, 144°30′E	♂	915	−20.16	8.51
¥6675	1986 4 27	39°30′N, 144°30′E	♀	870	−20.23	8.22
¥6676	1986 4 27	39°30′N, 144°30′E	♀	770	−21.20	8.52
¥6677	1986 4 27	39°30′N, 144°30′E	♀	900	−20.11	8.81
¥6678	1986 4 27	39°30′N, 144°30′E	♂	900	−19.06	9.98
¥6679	1986 4 27	39°30′N, 144°30′E	♂	770	−20.64	9.83
¥6680	1986 4 27	39°30′N, 144°30′E	♂	940	−19.47	9.92
¥6681	1986 4 27	39°30′N, 144°30′E	♂	900	−20.75	8.65
¥6682	1986 4 27	39°30′N, 144°30′E	♀	830	−19.75	9.88
¥6683	1986 4 27	39°30′N, 144°30′E	♂	880	−19.86	9.79
		Western subtropical Pacific in June				
B2520	1990 6 29	39°44′N, 176°45′W	♂	785	−18.15	11.87
B2571	1990 6 25	39°33′N, 172°55′E	♂	750	−17.62	10.45
B2572	1990 6 25	39°33′N, 172°55′E	♀	735	−18.22	12.96
B2739	1990 6 6	38°27′N, 179°32′W	♀	760	−18.62	8.44
B2740	1990 6 6	38°27′N, 179°32′W	♂	720	−19.21	10.28
B2821	1990 6 3	38°19′N, 179°20′E	♀	730	−17.67	11.84
B3345	1990 6 7	37°58′N, 155°00′E	♂	685	−19.16	10.52
B3346	1990 6 7	37°58′N, 155°00′E	♀	730	−19.70	10.60

APPENDIX 2. The sampling dates, sampling locations, measurements of body and $\delta^{13}C$, $\delta^{15}N$ values for Short-tailed Shearwaters.

Sample code	Date	Location	Sex	Body weight (g)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
		Pacific coast of northern Japan in April and May				
Y6688	1986 4 24	40°30′N, 143°30′E	♂	610	−22.35	8.21
Y6689	1986 4 24	40°30′N, 143°30′E	♀	615	−24.51	7.59
Y6690	1986 4 24	40°30′N, 143°30′E	♂	565	−23.30	8.19
B1556	1989 4 25	39°30′N, 144°30′E	♀	500	−23.18	7.36
B1559	1989 4 25	39°30′N, 144°30′E	♂	490	−24.31	7.33
B1562	1989 4 25	39°30′N, 144°30′E	♀	610	−24.48	7.37
B1557	1989 4 25	39°30′N, 144°30′E	♀	470	−21.53	8.25
B1558	1989 4 25	39°30′N, 144°30′E	♂	550	−22.97	7.93
B1560	1989 4 25	39°30′N, 144°30′E	♀	530	−23.14	7.42
B1561	1989 4 25	39°30′N, 144°30′E	♂	510	−20.51	8.09
Y6684	1986 5 1	41°34′N, 146°51′E	♂	645	−23.27	8.12
Y6685	1986 5 1	41°34′N, 146°51′E	♀	645	−22.60	8.76
Y6715	1986 5 10	40°07′N, 145°10′E	♂	590	−23.71	7.41
Y6720	1986 5 5	41°00′N, 145°00′E	♂	545	−23.32	8.24
Y6721	1986 5 5	41°00′N, 145°00′E	♂	465	−23.02	8.29
Y6722	1986 5 5	41°00′N, 145°00′E	♂	525	−22.88	8.83
Y6723	1986 5 5	41°00′N, 145°00′E	♀	575	−22.44	8.62
Y6724	1986 5 5	41°00′N, 145°00′E	♀	525	−23.88	7.42
Y6725	1986 5 5	41°00′N, 145°00′E	♀	525	−22.58	8.52
B1726	1989 5 2	40°30′N, 146°30′E	♀	440	−22.85	8.14
B1742	1989 5 3	41°30′N, 146°30′E	♀	520	−23.07	7.76
B1739	1989 5 3	41°30′N, 146°30′E	♀	535	−22.76	8.16
B1740	1989 5 3	41°30′N, 146°30′E	♀	475	−22.88	7.96
B1745	1989 5 3	41°30′N, 146°30′E	♂	535	−23.54	7.78
		Western subtropical Pacific in June				
B3347	1990 6 7	37°58′N, 155°00′E	♂	415	−19.93	11.77
B3348	1990 6 7	37°58′N, 155°00′E	♀	455	−19.43	11.07
B3349	1990 6 7	37°58′N, 155°00′E	♂	440	−19.89	12.17
B3350	1990 6 7	37°58′N, 155°00′E	♀	415	−19.40	11.47
		Western subarctic Pacific in June				
B1746	1989 6 9	45°30′N, 171°30′E	♂	410	−19.75	11.03
B1747	1989 6 9	45°30′N, 171°30′E	♀	450	−19.99	11.85
B1748	1989 6 9	45°30′N, 171°30′E	♀	385	−19.76	11.51
B1749	1989 6 9	45°30′N, 171°30′E	♂	420	−20.24	11.12
B1750	1989 6 9	45°30′N, 171°30′E	♀	370	−18.96	11.59
B1752	1989 6 9	45°30′N, 171°30′E	♂	400	−20.11	11.44
B1753	1989 6 9	45°30′N, 171°30′E	♀	430	−19.75	12.01
B1754	1989 6 9	45°30′N, 171°30′E	♂	420	−20.12	11.51
B1553	1989 6 19	46°30′N, 170°30′E	♂	510	−21.16	11.49
B1554	1989 6 19	46°30′N, 170°30′E	♂	640	−21.96	9.52
B1555	1989 6 19	46°30′N, 170°30′E	♀	400	−20.91	10.91
B1762	1989 6 8	45°30′N, 170°30′E	♂	450	−19.86	11.22
B1763	1989 6 8	45°30′N, 170°30′E	♀	395	−19.52	11.81
B1765	1989 6 8	45°30′N, 170°30′E	♀	435	−20.25	11.72
B1766	1989 6 8	45°30′N, 170°30′E	♀	440	−20.05	12.06
B3276	1990 6 17	46°30′N, 172°30′E	♂	490	−19.85	12.05