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Low $\delta^{13}C$ signatures in pelagic seabirds: lipid ingestion as a potential source of ^{13}C-depleted carbon in the Procellariiformes

D. R. Thompson[1,*], R. A. Phillips[2,], F. M. Stewart[3,***], S. Waldron[4]**

[1]Institute of Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, Scotland, UK
[2]Wildfowl and Wetlands Trust, Caerlaverock, Dumfriesshire DG1 4RS, Scotland, UK
[3]School of Environmental and Marine Sciences, University of Auckland, Tamaki Campus, Private Bag 92019, Auckland, New Zealand
[4]Scottish Universities Environmental Research Centre, Scottish Technology Park, East Kilbride, Glasgow G75 0QF, Scotland, UK

ABSTRACT: Stable-isotope ratios of carbon ($\delta^{13}C$) were determined in liver samples from a number of procellariiform seabirds from New Zealand. Generally, $\delta^{13}C$ values were low (depleted in ^{13}C) and there was a significant degree of intra- and inter-specific variation. We suggest that the pelagic versus inshore/benthic foraging model for $\delta^{13}C$ values in marine consumers is insufficient to explain the intra- and inter-specific variation. Nor can observed $\delta^{13}C$ values of procellariforms be linked to variation in foraging distances. We propose that carbon relatively depleted in ^{13}C derived from dietary lipids is incorporated into proteins. Support for this hypothesis is provided by depleted $\delta^{13}C$ signatures we measured in lipids extracted from liver tissue, which were always lower than $\delta^{13}C$ signatures in liver tissue (by 4.2 to 6.8‰, depending on species). Additionally, $\delta^{13}C$ values were determined in a small number of stomach-oil samples; these too were relatively depleted and lower than $\delta^{13}C$ values measured in liver tissue. Incorporation of dietary lipids, relatively depleted in ^{13}C, into protein could explain both intra- and inter-specific variation in $\delta^{13}C$ signatures in procellariiforms and may represent an additional explanation for relatively low $\delta^{13}C$ values in pelagic consumers.

KEY WORDS: Stable isotopes · Diet · New Zealand · Seabird · Foraging

INTRODUCTION

Stable-isotope ratios of consumer proteins reflect those of their prey in a predictable manner (DeNiro & Epstein 1978, 1981, Peterson & Fry 1987). Largely as a result of this, stable-isotope analysis has become an increasingly popular tool in ecological research, particularly to elucidate trophic relationships and to identify and quantify sources of dietary material within food chains. Analysis of stable carbon isotope ratios ($^{13}C/^{12}C$, conventionally expressed as $\delta^{13}C$) of consumers has been used to delineate between food assimilated from isotopically different sources. The proportion of marine versus freshwater or terrestrial food consumed by birds can be quantified, because $\delta^{13}C$ values in these ecosystems are markedly divergent due to differences in the incorporation of carbon during photosynthesis (e.g., Hobson 1987, 1990, Mizutani et al. 1990, Hobson & Sealy 1991).

Within the marine environment, $\delta^{13}C$ signatures have been further employed to differentiate between biota, including seabirds, utilising pelagic versus inshore/benthic food chains. Seabirds that feed pelag-

Present addresses:
*National Institute of Water and Atmospheric Research, 301 Evans Bay Parade, Greta Point, PO Box 14-901, Kilbirnie, Wellington, New Zealand.
E-mail: d.thompson@niwa.cri.nz
**British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK
***The Glasgow Academy, Colebrooke Street, Glasgow G12 8HE, Scotland, UK

ically exhibit relatively low $\delta^{13}C$ values compared to those species that feed benthically or in inshore environments (Hobson 1993, Hobson et al. 1994, Jarman et al. 1996, Sydeman et al. 1997, Thompson et al. 1999). The traditional explanation for this pattern is based on physical discrimination of stable carbon isotopes. This is thought to depend on the thickness of the boundary layer of water surrounding algae, which has been shown to ultimately determine the rate of CO_2 or HCO_3^- diffusion (Smith & Walker 1980). Benthic algae tend to be surrounded by well-defined and relatively thick boundary layers, due to relatively low water turbulence. This results in increased localised concentrations of ^{13}C that would otherwise be discriminated against. Increased availability of ^{13}C for photosynthesis leads to relatively elevated $\delta^{13}C$ values in benthic algae. In contrast, pelagic algae tend to be surrounded by relatively thin boundary layers due to increased water turbulence, to discriminate against ^{13}C, and therefore to exhibit relatively low $\delta^{13}C$ values (Smith & Walker 1980). In a recent review of the literature, France (1995) reported that this phenomenon was widespread, and that coastal fauna utilising benthic carbon sources were enriched in ^{13}C by, on average, 5‰ compared to fauna dependent on pelagic phytoplankton sources. Hobson et al. (1995) suggested that this boundary layer effect may be a key factor in determining the observed enrichment in ^{13}C in benthic organisms that was previously attributed to bacterial or meiofaunal processes (McConnaughey & McRoy 1979, Dunton et al. 1989).

To investigate the trend of relatively low $\delta^{13}C$ signatures in pelagic biota, we present $\delta^{13}C$ data for a range of procellariiform seabirds from the New Zealand region. Procellariiforms are a truly pelagic order of seabirds (Warham 1990). Specifically, we examine the extent of depletion in ^{13}C in this group, for which the influence of benthically fixed carbon should be minimal, and we assess whether patterns of $\delta^{13}C$ signatures in procellariiforms can be related to the distance at which birds forage from the colony. Finally, we present a novel hypothesis, based on $\delta^{13}C$ signatures in lipids, which may explain the relatively low $\delta^{13}C$ signatures and the inter-specific variation in $\delta^{13}C$ signatures in these pelagic consumers.

MATERIALS AND METHODS

Sample collection and preparation. The seabirds in this study were obtained as a by-catch of the longline tuna fishing industry around New Zealand in 1995 and 1996. Drowned birds were removed from fishing gear at sea, tagged and recorded by observers when landed on the vessel, and then flash-frozen. On arrival in port the birds were transferred to the Natural History Unit, Museum of New Zealand, Wellington. Birds were defrosted overnight before dissection of liver tissue using stainless steel instruments. Tissue samples were refrozen.

The seabirds analysed in the present study comprised the following species, with sample sizes in parentheses (taxonomic classification follows that in Turbott 1990, with the exception of small albatrosses, which follows that proposed by Nunn et al. 1996): southern royal albatross *Diomedea epomophora epomophora* (3), northern royal albatross *D. epomophora sandfordi* (1), wandering albatross *D. exulans antipodensis* (5), *D. exulans gibsoni* (4), white-capped albatross *Thalassarche cauta steadi* (40), New Zealand black-browed albatross *T. melanophrys impavida* (5), southern Buller's albatross *T. bulleri bulleri* (25), southern giant petrel *Macronectes giganteus* (1), sooty shearwater *Puffinus griseus* (7), white-chinned petrel *Procellaria aequinoctialis* (26), black petrel *P. parkinsoni* (2), grey petrel *P. cinerea* (6), cape petrel *Daption capense capense* (1), fairy prion *Pachyptila turtur* (2), grey-faced petrel *Pterodroma macroptera gouldi* (1) and black-bellied storm petrel *Fregetta tropica* (1).

Prior to stable-isotope analysis, frozen liver samples were allowed to thaw, and then dried to constant mass in an oven at 50°C. Dried liver samples were milled to an extremely fine powder with a stainless steel impactor operating at liquid nitrogen temperature (–196°C). Finally, lipids were removed from ground samples using refluxing chloroform in a Soxhlet apparatus, and then re-dried to constant mass as described above.

In addition to lipid-free liver tissue, $\delta^{13}C$ signatures were determined in extracted lipids from a sub-set of liver samples. Total lipids were removed from liver tissue in the following species, (sample sizes in parentheses): northern royal albatross (1), white-capped albatross (4), New Zealand black-browed albatross (1), southern Buller's albatross (4), sooty shearwater (4), white-chinned petrel (4), black petrel (2), grey petrel (3) and grey-faced petrel (1). In all cases, dried and ground liver tissue (see above) was wrapped in precombusted glass-fibre filter paper and placed in excess petroleum ether solvent in a cleaned glass beaker for 4 h. The beaker was covered with parafilm and the contents swirled regularly during this period. Most solvent was evaporated initially in a fume cupboard, then beakers were transferred to a vacuum oven at 40°C for 48 h, leaving lipids as a residue. Dried samples were stored in air-tight glass vials prior to isotope analysis.

Finally, we obtained a small number of stomach-oil samples from procellariiforms killed at sea by fishing gear and brought back to land for further processing. The majority of stomachs examined contained either

remnants of partly digested food or were completely empty, and when oil was present it was often mixed with food remnants and aqueous fractions (C. J. R. Roberston pers. comm.). Oil samples were collected from 4 white-capped albatross, 1 black-browed albatross *Thalassarche melanophrys melanophrys* and 1 grey petrel. Moisture was removed by placing oil samples in a warm oven (40°C) for 24 h, and samples were stored in air-tight glass vials prior to stable-isotope analysis.

Stable-isotope analysis. All isotopic measurements were determined using a Carlo Erba C/N/S analyser linked to a Finnigan Tracer Matt mass spectrometer. Isotope ratios are expressed conventionally as δ values in parts per thousand (‰) according to the following equation:

$$\delta^{13}C = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000$$

where R_{sample} is the ratio $^{13}C/^{12}C$. $R_{standard}$ for ^{13}C is PeeDee Belemnite (PDB). All groups of analyses included standard reference materials for routine quality control. The majority of samples were determined in triplicate, or at least in duplicate. In all cases, the mean of replicate analyses was determined. Analytical precision was ±0.2‰. Shapiro-Wilk *W*-tests were performed to determine whether samples conformed to a normal distribution, and 1-way ANOVA with Scheffé range tests were used to explore inter-specific differences in mean $\delta^{13}C$ signatures.

RESULTS

Where samples sizes were sufficiently large, Shapiro-Wilk *W*-tests revealed that the distribution of $\delta^{13}C$ values did not differ significantly from normal ($p > 0.05$ in all cases). Mean $\delta^{13}C$ values in lipid-free liver and in lipid extracted from liver, together with ranges, for all species are presented in Table 1. Inter-specific variation in $\delta^{13}C$ values in liver tissue was significant (1-way ANOVA: $F_{15,113} = 5.57$, $p < 0.001$). Scheffé range tests revealed that the mean $\delta^{13}C$ value in sooty shearwaters was significantly lower ($p < 0.05$) than mean $\delta^{13}C$ values for shy albatross, southern Buller's albatross and white-chinned petrel (Table 1). The most enriched $\delta^{13}C$ value was found in the single northern royal albatross (–17.4‰), whilst the most depleted $\delta^{13}C$ signature was recorded in a sooty shearwater (–21.9‰), a total range of values spanning 4.5‰ (Table 1). In all cases, $\delta^{13}C$ signatures in lipids extracted from liver tissue were lower (depleted in ^{13}C) compared to $\delta^{13}C$ values in lipid-free liver tissue (by 4.2 to 6.8‰, depending on species), with no overlap in values for any species (Table 1).

Stomach-oil samples obtained from 6 individuals of 3 species exhibited relatively depleted $\delta^{13}C$ signatures. Oil from white-capped albatross had a mean $\delta^{13}C$ value of –22.2‰ (n = 4, SD = 4.4), from a single black-browed albatross –23.1‰, and from a single grey petrel –24.4‰.

DISCUSSION

The $\delta^{13}C$ signatures presented in the present study (Table 1) were similar to $\delta^{13}C$ measurements generated by other studies of procellariiform seabirds. A compilation of published $\delta^{13}C$ data in procellariiforms is presented in Table 2. Whilst diet to tissue fractionation factors ($\Delta^{13}C_{diet\text{-}tissue}$) may differ slightly for different tissues, the overall pattern is one of relatively low $\delta^{13}C$ values in a range of species from widely separated locations (Table 2). Particularly noteworthy are the extremely low $\delta^{13}C$ signatures reported in muscle tissue from short-tailed shearwaters *Puffinus tenuirostris* from the Pacific, in which mean values ranged from –23.0 to –19.7‰, depending on sampling location (Minami et al. 1995), 2 species of storm-petrel from the Gulf of Alaska, mean $\delta^{13}C$ values = –21.2 and –21.5‰ (Hobson et al. 1994), and sooty shearwaters, for which values as low as –21.2‰ were reported from northern Japan (Minami et al. 1995: Table 2).

There is clearly a strong trend for low $\delta^{13}C$ values in pelagic seabirds such as procellariiforms (this study and others cited in Table 2), and more elevated $\delta^{13}C$ signatures in other species. This pattern agrees with the predictions of the pelagic versus inshore/benthic foraging model for $\delta^{13}C$ values based on boundary-layer diffusion effects (France 1995, Hecky & Hesslein 1995), and is in keeping with the extremely pelagic nature of procellariiform seabirds (Warham 1990).

However, although the $\delta^{13}C$ values reported here for procellariiforms were relatively low, the inter-specific variation in $\delta^{13}C$ signatures was significant, and the overall spread of values (4.5‰: Table 1) was very similar to that noted by France (1995) between marine consumers reliant on pelagic phytoplankton and marine consumers reliant on benthic algae as carbon sources (ca 5‰). In other words, the range of $\delta^{13}C$ signatures reported here for exclusively pelagic foragers corresponded to that between pelagic and inshore/benthic foragers. All samples in the present study were obtained from the same general location (New Zealand), and all the species in the present study are wholly pelagic, with no evidence of feeding on prey reliant on benthic algae as a carbon source (see Marchant & Higgins 1990 for dietary information). It would therefore seem reasonable to conclude that the variance in $\delta^{13}C$ values within this group cannot be

explained solely by the pelagic versus inshore/benthic foraging model described above.

One explanation for the relatively wide range of $\delta^{13}C$ values in procellariiforms (Table 1) could be that $\delta^{13}C$ signature varies in a way that can be linked to the foraging characteristics of a particular species, i.e., those species which feed the farthest from the colony might exhibit the most depleted $\delta^{13}C$ values, as in previous studies of $\delta^{13}C$ and foraging in seabirds, although not exclusively procellariiforms (Hobson 1993, Hobson et al. 1994, Jarman et al. 1996, Sydeman et al. 1997, Thompson et al. 1999). However, there is little evidence to support this idea in the present study, not least because procellariiforms are able to forage over an extremely wide range of distances from the breeding colony, and can vary foraging strategies over the course of a breeding season (Weimerskirch 1997). Linking $\delta^{13}C$ signatures in procellariiforms with foraging distance is further complicated by the fact that many species adopt a foraging strategy that includes discrete, relatively short trips interspersed with relatively long trips, covering correspondingly short and long distances from the breeding site (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994, 1995, 1997, Weimerskirch 1998, Weimerskirch & Cherel 1998, Waugh et al. 1999). Additionally, stable-isotope signatures in pelagic seabirds have been shown to vary depending on latitude, with relatively well-defined shifts in isotope signature across frontal boundaries (Cherel et al. 2000). Based on the available information, we conclude that the evidence that interspecific variation in $\delta^{13}C$ signatures of procellariiforms can be linked to the extent of pelagic foraging is unconvincing.

Alternatively, we propose that ingestion of lipid-derived carbon and its assimilation into protein serves as an additional factor which is likely to contribute to the relatively low $\delta^{13}C$ values in procellariiforms, and also to the variance in $\delta^{13}C$ values between and within species. All procellariiforms (with the notable excep-

Table 1. Stable carbon-isotope signatures of lipid-free liver tissue and lipid extracted from liver of procellariiform seabirds from the New Zealand region. Values are means ±1 SD (where number analysed > 2). Identical superscripts indicate no significant difference between lipid-free liver values as determined using Scheffé range tests at $p < 0.05$ level. na: not analysed

Species	Lipid-free liver			Extracted lipid		
	No. analysed	$\delta^{13}C$ (‰)	Range (‰)	No. analysed	$\delta^{13}C$ (‰)	Range (‰)
Southern royal albatross *Diomedea epomophora epomophora*	3	$-18.9^{a,b} \pm 0.5$	−19.4 to −18.4	na		
Northern royal albatross *Diomedea epomophora sandfordi*	1	$-17.4^{a,b}$		1	−23.8	
Wandering albatross *Diomedea exulans antipodensis*	5	$-19.2^{a,b} \pm 0.7$	−20.4 to −18.5	na		
Wandering albatross *Diomedea exulans gibsoni*	4	$-19.2^{a,b} \pm 0.4$	−19.8 to −18.9	na		
White-capped albatross *Thalassarche cauta steadi*	40	$-19.1^{b} \pm 0.5$	−20.1 to −17.7	4	−24.2 ± 0.7	−25.1 to −23.4
New Zealand black-browed albatross *Thalassarche melanophrys impavida*	5	$-19.4^{a,b} \pm 0.7$	−20.5 to −18.8	1	−23.6	
Southern Buller's albatross *Thalassarche bulleri bulleri*	25	$-18.9^{b} \pm 0.6$	−19.9 to −17.6	4	−24.4 ± 0.4	−24.8 to −24.0
Southern giant petrel *Macronectes giganteus*	1	$-20.7^{a,b}$		na		
Sooty shearwater *Puffinus griseus*	7	$-20.6^{a} \pm 1.2$	−21.9 to −19.2	4	−25.2 ± 0.5	−25.8 to −24.6
White-chinned petrel *Procellaria aequinoctialis*	25	$-19.3^{b} \pm 0.4$	−20.4 to −18.7	4	−24.9 ± 1.1	−26.5 to −24.1
Black petrel *Procellaria parkinsoni*	2	$-18.2^{a,b}$	−18.2 to −18.1	2	−25.0	−25.5 to −24.5
Grey petrel *Procellaria cinerea*	6	$-19.4^{a,b} \pm 0.5$	−19.9 to −18.7	3	−24.0 ± 1.1	−24.8 to −22.8
Cape petrel *Daption capense capense*	1	$-20.7^{a,b}$		na		
Fairy prion *Pachyptila turtur*	2	$-19.7^{a,b}$	−19.8 to −19.5	na		
Grey-faced petrel *Pterodroma macroptera gouldi*	1	$-18.3^{a,b}$		1	−23.3	
Black-bellied storm petrel *Fregetta tropica*	1	$-19.5^{a,b}$		na		

Table 2. Compilation of $\delta^{13}C$ data in procellariiform seabirds. –: no data

Species	Location	Tissue	No. analysed	Mean $\delta^{13}C$ (‰)	Range $\delta^{13}C$ (‰)	Source
Short-tailed albatross						
Phoebastria albatrus	Torishima Is., southern Japan	Feathers	2[a]	–16.6	–	Mizutani & Wada (1988)
Laysan albatross						
Phoebastria immutabilis	North Pacific	Muscle	28	–18.9	–19.6 to –18.0	Gould et al. (1997)
Black-footed albatross						
Phoebastria nigripes	North Pacific	Muscle	20	–18.1	–20.5 to –17.0	Gould et al. (1997)
Black-browed albatross						
Thalassarche melanophrys	Kerguelen Is., southern Indian Ocean	Feathers	40	–18.0 to –17.3[b]	–	Cherel et al. (2000)
Northern fulmar						
Fulmarus glacialis	Arctic Canada	Muscle	25	–19.2	–	Hobson & Welch (1992)
	Arctic Canada	Muscle	16	–19.2[c]	–	Hobson (1993)
	Northeast Atlantic	Muscle	5	–18.1	–18.7 to –17.8	Thompson & Furness (1995)
	Northeast Atlantic	Bone collagen	5	–15.3	–15.7 to –15.0	Thompson & Furness (1995)
	Northeast Atlantic	Body feathers	30	–17.3	–	Thompson et al. (1995)
Sooty shearwater						
Puffinus griseus	Pacific coast, northern Japan	Muscle	10	–20.1	–21.2 to –19.2	Minami et al. (1995)
	Western subtropical Pacific	Muscle	8	–18.5	–19.7 to –17.6	Minami et al. (1995)
	Northeast Pacific	Muscle	12	–19.6	–	Minami & Ogi (1997)
	Northwest Pacific	Muscle	4	–20.2	–	Minami & Ogi (1997)
Short-tailed shearwater						
Puffinus tenuirostris	Pacific coast, northern Japan	Muscle	24	–23.0	–24.5 to –20.5	Minami et al. (1995)
	Western subtropical Pacific	Muscle	4	–19.7	–19.9 to –19.4	Minami et al. (1995)
	Western subarctic Pacific	Muscle	16	–20.1	–22.0 to –19.0	Minami et al. (1995)
Leach's storm petrel						
Oceanodroma leucorhoa	Gulf of Alaska	Muscle	5	–21.2	–	Hobson et al. (1994)
Fork-tailed storm petrel						
Oceanodroma furcata	Gulf of Alaska	Muscle	1	–21.5[c]	–	Hobson et al. (1994)

[a]Two analyses, number of individuals not stated
[b]Range of 4 means, depending on feather type and year
[c]Estimated value from figure

tion of diving petrels, family Pelecanoididae) possess stomach oils. These have been demonstrated to be of dietary origin, and to show considerable inter-specific variation in composition (Cheah & Hansen 1970, Clark & Prince 1976, Warham et al. 1976, Warham 1977). Procellariiforms concentrate lipids in digesta to form stomach oil (Place et al. 1989), one of the primary functions of which is to serve as an extremely rich energy source (Warham 1977, Taylor et al. 1997). Lipids are relatively depleted in ^{13}C compared to other tissues, and consequently exhibit relatively low $\delta^{13}C$ signatures (McConnaughey & McRoy 1979, Tieszen et al. 1983, Schell et al. 1989, Hobson et al. 1997). The relatively low $\delta^{13}C$ signatures measured in lipids extracted from liver tissue, and in the small number of stomach-oil samples from procellariiforms (see Table 1 and 'Results') confirm lipids as a source of relatively ^{13}C-depleted carbon.

Perhaps most importantly, biochemical pathways exist whereby carbon of lipid origin can be incorporated into amino acids and hence protein. For example, oxidation of dietary lipids results in the production of acetyl coenzyme A. Acetyl coenzyme A is oxidised in the TCA cycle, where in turn, alpha-ketoglutarate and oxaloacetate are formed. The latter will also form pyruvate. These are the keto-acids of glutamate, aspartate and alanine, respectively. From here all non-essential amino acids can be produced with varying degrees of lipid-derived carbon (Mathews & van Holde 1990).

Hence, there exists a mechanism by which procellariiform seabirds can incorporate lipid-carbon, depleted in ^{13}C, into proteins. Relatively low $\delta^{13}C$ values in this group (Tables 1 & 2) are entirely consistent with this mechanism. Furthermore, we would anticipate that inter-specific differences in $\delta^{13}C$ signatures would exist, based on diet, given the marked variation in chemical composition of oils in different species (Clark & Prince 1976, Warham et al. 1976). Interestingly, Muir et al. (1995) suggested that low $\delta^{13}C$ values in some walrus *Odobenus rosmarus* from Canada could have resulted from consumption of seal blubber, a ^{13}C-depleted food resource.

In conclusion, assimilation of carbon from dietary lipids, relatively depleted in ^{13}C, provides an explanation for low $\delta^{13}C$ values and for inter- and intra-specific variation in $\delta^{13}C$ values in procellariiform seabirds, in addition to that provided by consumption of carbon fixed by pelagic phytoplankton. The importance of dietary, lipid-derived carbon in determining consumer $\delta^{13}C$ values may not be confined to procellariiforms, but may also apply to other seabirds and marine mammals. Compound-specific carbon stable-isotope analysis would help to elucidate this process further, and would enhance the application of carbon-isotope analysis to studies of diet in marine consumers.

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