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Trophic segregation of Falkland Islands seabirds: insights from stable isotope analysis

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Abstract Seabird colonies provide rare opportunities to study trophic segregation in an entire bird community. We here present data on nitrogen and carbon isotope ratios of eight species of seabirds from New Island, Falkland Islands, and compare trophic levels (TL) and foraging distributions. We included adult feathers representing the interbreeding season, as well as chick feathers or down representing the breeding season. The stable isotope ratios indicated differences in feeding areas and TLs between species, consistent with the data of previous conventional diet analyses and observations at sea. We further reviewed conventional and stable isotope seabird community studies calculating the means and ranges of TLs observed across these studies. The mean TL (3.7) of the seabird community on New Island was at the lower end of the mean value range (3.5–4.5), but not significantly different, from the reviewed seabird communities. Seabirds on New Island had a range of 1.3 TLs, which is on the upper end of ranges within a community (0.4–1.5), indicating strong trophic structuring.

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Introduction

Seabird colonies have become a focus of international conservation due to the increasing interaction with fisheries, high mortality rates related to anthropogenic activity and vulnerability to climate change (Thompson 1989; Barton 2002; Hilton et al. 2006). The correct interpretation of long-term population-trends depends not only on a good knowledge of the breeding and foraging biology of the species, but also on additional monitoring of diet. Classical methods of diet analysis such as stomach flushing, dissection and pellet analysis (Barret et al. 2007) have been extensively applied to seabirds in various colonies (Wanless et al. 1992; Croxall et al. 1997; Cherel et al. 2002; Clausen and Pütz 2002). However, those methods are biased against easily digested prey (Hobson et al. 1994) and can be stressful for the birds or require dead birds. In addition, these conventional methods are often difficult to apply during the interbreeding season (but see Jackson 1988), diet analysis can be very time-consuming and sampling can be restricted by the need to transport stomach contents frozen or in ethanol.

Stable isotope ratios of bird tissues and prey organisms can be used to overcome these problems (Hobson et al. 1994; Post 2002; Fry 2006), and can be applied to complement other available methods. The stable nitrogen isotope ^{15}N is enriched relative to ^{14}N in a predictable manner with each trophic level (TL), providing a tool to estimate TLs (Post 2002). Due to different turnover times, different tissues integrate diet over more or less time, thereby buffering fluctuations in the diet (Ogden et al. 2004). As the

isotope value of the feathers remains unchanged after they are grown, feathers provide a tool to study diet during the moulting period, which procellariiform seabirds usually spend at sea (Cherel et al. 2000a). The heavy isotope of carbon ^{13}C is only slightly enriched (in relation to ^{12}C) with each trophic step, providing little information about TL (Hobson and Welch 1992; Post 2002). However, it is a good tracer of feeding areas in the southwest Atlantic, as it changes with latitude (Quillfeldt et al. 2005; Cherel and Hobson 2007). Carbon isotope ratios are lower in waters south of the Antarctic Convergence. In addition, carbon isotope ratios are higher in areas of high productivity and lower in pelagic phytoplankton than in benthic and inshore phytoplankton (Francois et al. 1993; Hobson et al. 1994; Quillfeldt et al. 2005; Cherel and Hobson 2007) and these factors can result in variations that overprint the linear latitude-related effect.

The diet of several seabird species of New Island, Falkland Islands, has been studied on two occasions using conventional methods (Thompson 1989; Clausen and Pütz 2002). The aim of the present study was to quantify trophic segregation within the seabird community, as reflected in stable isotope ratios, and to compare TLs with recent studies on diet composition on New Island and with other colonies.

Methods

Species and study site

Samples were collected as part of an ongoing study at New Island Nature Reserve, Falkland Islands (51°43′S, 61°17′W; e.g., Quillfeldt et al. 2003, 2006, 2007a, b, c, 2008a, b, c, d) during three consecutive breeding seasons (2003/2004, 2004/2005, 2005/2006). New Island is recognised as an important bird area for its seabird colonies of 13 different species. The seabird community comprises 4(3) species of penguins, 1(1) albatross, 3(2) petrels, 2(1) cormorants, 1(0) skua and 2(1) gulls (in parentheses the number of species here studied). The weaker western branch of the Falkland Current produces a productive area of upwelling west of New Island (Fig. 1, oceanography reviewed by Upton and Shaw 2002; Glorioso 2002).

Sampling

We included samples representing the interbreeding season (adult feathers), as well as the breeding season (chick feathers or down where available). A total of 170 samples from eight species of seabirds were collected (Table 1). Feathers from albatrosses, petrels, prions, cormorants and gulls were collected non-invasively from birds during the
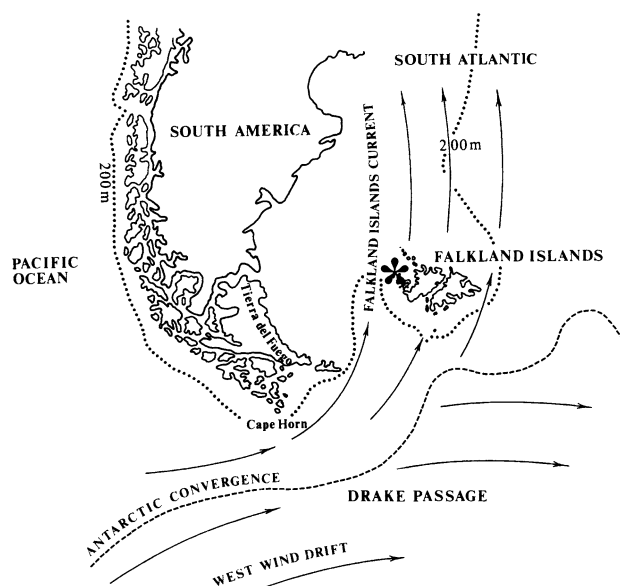
Fig. 1 Map of the study area. New Island is marked with a *star*

breeding season, by checking the area around breeding colonies for remains and moulted feathers. Feathers from penguins were collected during moult from the ground in front of individual burrows (Magellanic penguins *Spheniscus magellanicus*) or around moulting groups of rockhopper—*Eudyptes chrysocome* and gentoo penguins *Pygoscelis papua*. We cannot rule out completely that two moulted feathers of penguins are from the same bird but it is highly unlikely because several hundred to thousand birds moult in a group and we have collected a single feather from each site, with a minimum distance of 20 m between collection sites. Chick down from thin-billed prions *Pachyptila belcheri* and black-browed albatross *Thalassarche melanophrys* was collected during the time of natural shedding of these feathers, by gently pulling a small amount of down off the tips of the contour feathers to which they were attached. Down feathers of penguins were collected from remains of chicks killed by skuas. All feathers except the penguin feathers were clearly distinguished by size and colour. The three penguin species breed and moult in very different places, e.g., Magellanic penguins in their burrows where they also moult. Thus, feathers were collected at the burrow entrances. Gentoo penguins have two large colonies, each with several sub-colonies, on two plains at New Island. They return to these colonies to moult. Finally, rockhopper penguins breed and moult at three colonies on rock cliffs at New Island, and we collected feathers there, during the moulting time.

The Falkland Islands Fisheries Department kindly provided samples obtained during a survey cruise in February 2006 by bottom and plankton trawling close to the Falkland Islands (P. Brickle, personal communication). The samples

Table 1 Stable isotope ratios and calculated TLs of seabirds from New Island

Species	Tissue	$\delta^{13}C$ (‰)	SE	$\delta^{15}N$ (‰)	SE	TL	n
GEPE[a, b]	Feathers	−16.26	0.10	15.88	0.24	3.7	13
GEPE[a]	Down	−17.20	0.14	14.09	0.02	3.2	2
ROPE[c]	Feathers	−16.65	0.46	14.03	0.39	3.2	6
ROPE[c]	Down	−15.85	0.09	13.56	0.19	3.0	5
MAPE[a, b, c]	Feathers	−16.96	0.57	15.50	0.49	3.6	11
BBAL[a, c]	Feathers	−15.98	0.19	16.88	0.25	4.0	10
BBAL[a, c]	Down	−16.44	0.10	16.17	0.17	3.8	12
TBPR[b, c]	Feathers	−24.04	0.23	8.32	0.26		62
TBPR[b, c]	Down	−18.50	0.15	12.10	0.17		27
WCPE[c]	Feathers	−15.44	0.49	18.38	0.69	4.4	5
WCPE[c]	Down	−18.57	1.01	15.45	0.61	3.6	3
IMCO[c]	Feathers	−15.38	0.39	16.05	0.11	3.8	7
DOGU[b]	Feathers	−16.37	0.18	13.90	0.17	3.1	6

All feather samples are from adult birds, all down samples are from chicks

GEPE gentoo penguin *Pygoscelis papua*, *ROPE* rockhopper penguin *Eudyptes chrysocome*, *MAPE* Magellanic penguin *Spheniscus magellanicus*, *BBAL* black-browed albatross *Thalassarche melanophrys*, *TBPR* thin-billed prion *Pachyptila belcheri*, *WCPE* white-chinned petrel *Procellaria aequinoctialis*, *IMCO* imperial cormorant *Phalacrocorax atriceps*, *DOGU* dolphin gull *Larus scoresbii*

[a] Breeding season 2003/2004

[b] Breeding season 2004/2005

[c] Breeding season 2005/2006

included fish muscle from southern blue whiting *Micromesistius australis* (*n* = 2, length 470–560 mm), hoki *Macruronus magellanicus* (*n* = 4, length 270–380 mm), pike icefish *Champsocephalus esox* (*n* = 4, length 170–310 mm), yellowfin rockcod *Patagonotothen guntheri* (*n* = 4, length 150–160 mm) and Patagonian rockcod *Patagonotothen ramsayi* (*n* = 4, length 230–280 mm), squid muscle samples of Argentine shortfin squid *Illex argentinus* (*n* = 4, length 165 mm), great hooked squid *Moroteuthis ingens* (*n* = 4, length 180–230 mm) and Patagonian longfin squid *Loligo gahi* (*n* = 4, length 125–250 mm), as well as crustaceans (whole exemplars of krill *Euphausia lucens* and *Thysanoessa macrura,* lobster krill *Munida gregaria* and amphipods *Themisto gaudichaudii*). The stable isotope data of these samples are given in the appendices of Quillfeldt et al. (2008a). All of these species are particularly abundant representatives for crustaceans, squid and fish species around the Falkland Islands and are known from conventional diet analysis to be of great importance to the seabirds breeding on New Island (Thompson 1989). Some of the taxa are also important commercial species, especially *Lolligo gahi, Ilex argentinus* and *Micromesistius australis* (Agnew 2002).

Sample preparation and stable isotope analysis

Feather tips and down were cut into small pieces with stainless steel scissors. Lipids were not washed off the feathers as they were shown to have negligible effects on the isotope ratios (Mizutani et al. 1992).

Lipids were extracted from all fish, squid and crustacean samples, to control for differences in lipid content (Bearhop et al. 2002), using a Soxhlet apparatus with a methanol:chloroform 2:1 solvent. Following extraction, the samples were dried under a fume hood for at least 12 h and ground to a homogeneous fine powder with mortar and pestle.

Sub-samples of crustaceans were acid-washed with HCl after lipid extraction to remove inorganic carbonates (Carabel et al. 2006). Acid-washed sub-samples were used to determine the carbon isotope ratios of crustaceans.

Sub-samples of 0.7 mg were loaded in tin-cups for stable isotope analysis. Carbon and nitrogen isotope ratios were measured by continuous-flow isotope ratio mass spectrometry using a Costech Elemental Analyser linked to a Thermo Finnigan Delta Plus XP Mass Spectrometer. Carbon and nitrogen isotope ratios were determined simultaneously for feathers, but all tissues which had undergone lipid extraction and acid washing were analysed as two separate aliquots: untreated for nitrogen and treated tissue for carbon. Two laboratory standards were analysed for every 10 unknown samples, allowing any instrumental drift over a typical 14 h run to be corrected. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) deviation from the international standards V-Pee dee belemnite (carbon) and AIR (nitrogen), according to the following equation $\delta Y = (R_{sample} \times R_{standard}^{-1} - 1) \times 1{,}000$ where Y is ^{15}N or ^{13}C and R is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. Measurement precision of both $\delta^{15}N$ and $\delta^{13}C$ was better than 0.3‰.

Calculation of trophic levels

Animal tissues are enriched in ^{15}N compared to their diet (Mizutani et al. 1992; Post 2002; Fry 2006). The mean enrichment factor across various taxa in 56 studies was 3.4‰ ± 0.98 SD (Post 2002). The fractionation factor from diet to bird feathers is greater. The physiological principals causing the higher enrichment factor from diet to feather compared to from diet to blood or from diet to muscle tissue are not studied in most species, but higher enrichment factor from diet to feather is observed in various species including garden warbler *Sylvia borin* (Hobson and Bairlein 2003), white ibis *Eudocimus albus* and cormorant *Phalacrocorax carbo* (Mizutani et al. 1992). For penguins it is suspected, that this is due to the mobilisation of internal stores during moult (Cherel et al. 2005a;

Quillfeldt et al. 2008b). The mean enrichment factor in 20 controlled feeding experiments was 4.0‰ ± 1.2 SD (Cherel et al. 2005b), and paired differences in $\delta^{15}N$ of simultaneously grown feathers and blood cells of procellariiform seabirds were around 1.0‰ (Quillfeldt et al. 2008b). The TL of an animal (TLa) can be calculated in systems with only one primary producer by comparing its $\delta^{15}N$ value (SIa) with that of another taxon (SIb) of known TL (TLb) assuming an average enrichment of 3.4‰ (Post 2002):

$$TLa = TLb + (SIa-SIb) \times 3.4\%^{-1} \qquad (1)$$

To include the different fractionation factor for feathers (SIc) we subtracted SIc from the difference between SIa and SIb and added 1 to the trophic level of the reference species (TLb)

$$TLa = TLb + 1 + (SIa-SIb-SIc) \times 3.4\%^{-1} \qquad (2)$$

The TLs of birds (except adult thin-billed prions), fish and squid in the present study were calculated relative to nitrogen isotope ratios of *Euphausia lucens* and *Thysanoessa macrura* (mean $\delta^{15}N$ of both species was 10.51‰) with an estimated TL of 2.3 [determined for *E. superba* (Hodum and Hobson 2000)]. Euphausids are ideally suited as reference species because they are relatively long-lived compared to other species of zooplankton and feed largely on phytoplankton, thereby buffering possible fluctuations of isotope ratios in the phytoplankton (Sommer 1998; Post 2002). Several individuals were pooled in the samples of *E. lucens* and *T. macrura* to obtain a reliable average reference value.

Comparison with other studies

Several studies on trophic relationships in seabird colonies have been published, but the methods vary from study to study, especially the choice of tissue from the birds (muscle, liver, whole blood, egg albumen or feather), reference species for defining trophic levels [particulate organic matter (POM), euphausids, *Engraulis anchoita* (fish), *Calanus hyperboreus* (amphipod) or *Mallotus villosus* (fish)] and fractionation factor (2.4–3.3) (Thompson 1989; Hobson and Welch 1992; Rau et al. 1992; Hobson et al. 1994; Sydeman et al. 1997; Hobson et al. 2002; Forero et al. 2004). Therefore, we calculated new TLs from the published $\delta^{15}N$ values with a consistent model (Eq. 2). SIc was varied depending on the tissue: pectoral muscle 3.1‰, whole blood 2.9‰, liver 4.0‰, feather 4.0‰ (Ogden et al. 2004), and for egg albumen we used a discrimination factor of 3.1‰ (Sydeman et al. 1997). For TLb and SIa we choose published values for reference species from each study (Table 4). We also compared isotope ratios with results from conventional diet studies for all seabirds in this study. From the published

isotope ratios TLs were calculated with the model described above.

Data analysis

Data analysis was carried out using SPSS 11.0. The isotopic ratios were compared between groups using discriminant analysis (Wilk's λ) with carbon and nitrogen isotope ratios as dependent variables in order to detect overall differences based on both carbon and nitrogen isotope ratios. If overall differences were detected, $\delta^{15}N$ and $\delta^{13}C$ values were compared separately by one-way ANOVA, and Tukey post hoc tests. The TLs of seabird communities were compared with ANOVA and Tukey post hoc tests.

## Results

Prey type isotope ratios and trophic levels

Fish, squid and crustaceans collected in the vicinity of the Falkland Islands had distinct isotope ratios (Figs. 2, 3, Wilk's $\lambda = 0.31$, $P < 0.001$). Differences among the three groups were clearest in $\delta^{15}N$ values (ANOVA: $F_{34,2} = 22.4$, $P < 0.001$), where all pairwise comparisons (Tukey post hoc tests) were significant. There was also an overall difference between fish, squid and crustaceans in $\delta^{13}C$ values (ANOVA: $F_{34,2} = 5.5$, $P = 0.008$), where crustaceans had lower $\delta^{13}C$, while squid and fish had similar $\delta^{13}C$ (Tukey post hoc tests). The calculated TLs of fish ranged over 0.6 TL (mean 3.1, SE 0.1, min 2.8, max 3.4), squid ranged over 0.7 TL (mean 2.3, SE 0.2, min 1.9, max 2.6) and crustaceans ranged over 1.3 TL (mean 2.0, SE 0.2, min 1.1, max 2.4).

Seabird isotope ratios and trophic levels

The feathers of adult seabirds differed in isotope values between species (Wilk's $\lambda = 0.330$, $P < 0.001$), both in $\delta^{13}C$ (ANOVA: $F_{7,113} = 113.9$, $P < 0.001$) and $\delta^{15}N$ ($F_{7,113} = 64.2$, $P < 0.001$). Samples of adult thin-billed prions were separated by significantly lower $\delta^{13}C$ and $\delta^{15}N$ values than all other groups (Tukey post hoc tests, Table 1, Fig. 3) and showed a wide range of values both in $\delta^{13}C$ (min −28.07‰, max −18.27‰) and $\delta^{15}N$ (min 5.93‰, max 17.04‰). When thin-billed prions were excluded from the analysis, there was only a slight difference between species in $\delta^{13}C$ ($F_{6,52} = 2.7$, $P = 0.024$), as Magellanic penguins and imperial cormorants differed in $\delta^{13}C$ according to Tukey post hoc tests ($P = 0.025$).

When thin-billed prions were excluded, the feathers of adults of the remaining seabird species still differed in their
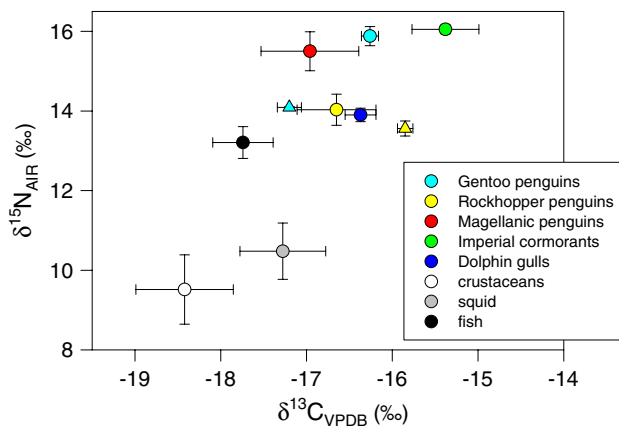
Fig. 2 Isotope ratios of penguins, imperial cormorants, dolphin gulls and prey classes (mean ± SE). Adult feathers, which are grown in the interbreeding period, are marked with *circles*. Chick down feathers, which are grown in the breeding season, are given in *triangles*
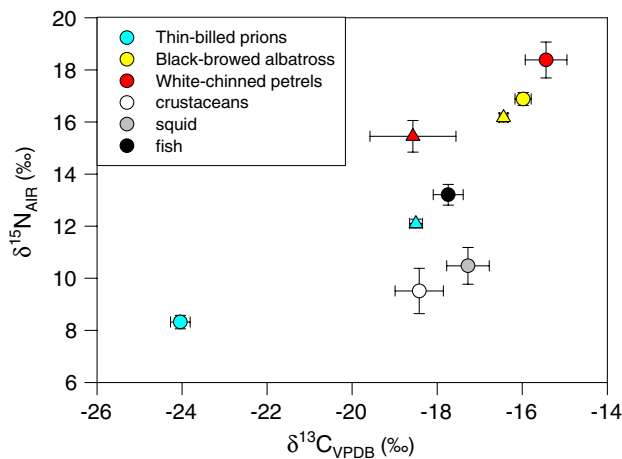

Fig. 3 Isotope ratios of procellariiform seabirds and prey classes (mean ± SE). Adult feathers, which are grown in the interbreeding period, are marked with *circles*. Chick down feathers, which are grown in the breeding season, are given in *triangles*

δ^{15}N values ($F_{6,52}$ = 5.1, P < 0.001), with the highest values observed in white-chinned petrels and black-browed albatross, and the lowest values for dolphin gulls (Fig. 4; Table 1).

Adults of the three penguin species differed in their isotope signatures (Fig. 2, Wilk's λ = 0.068, P = 0.037), and this was due to differences in δ^{15}N ($F_{2,27}$ = 4.9, P = 0.016). Post hoc tests identified rockhopper penguins as different in δ^{15}N from the other two species (Tukey, P = 0.012). Adults of the three penguin species had similar δ^{13}C (ANOVA: $F_{2,27}$ = 0.9, P = 0.410).

Differences between adults and chicks were tested for five species. The significance level was adjusted to P = 0.01 according to Bonferroni. Compared with adults, gentoo penguin chicks had significantly lower δ^{13}C values
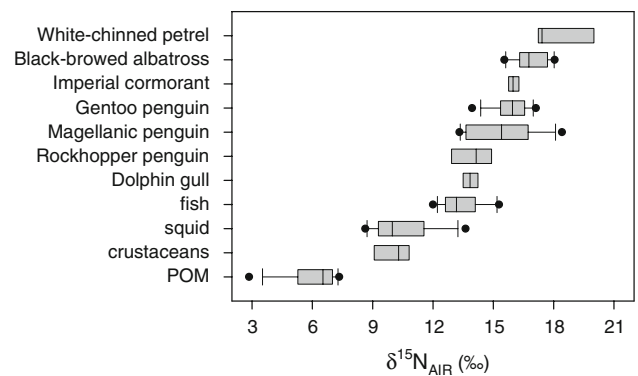
Fig. 4 Nitrogen stable isotope ratios of seabirds (adult feathers) and prey species categories. The *grey area* encloses the second and third quartiles. *Black bars* depict the first and fourth quartile. Outlying data are indicated by *black dots*. Thin-billed prions were omitted because of the different baseline isotope value due to their southern distribution

(*t* test: t = 3.5, *df* 13, P = 0.004) and non-significantly lower δ^{15}N values (*t* test: t = 2. 8, *df* 13, P = 0.014). In thin-billed prions, the opposite was observed, as feathers of adults were significantly depleted in ^{13}C and ^{15}N compared to down feathers of chicks (Fig. 3, δ^{13}C: t = 15.3, *df* 87, P < 0.001; δ^{15}N: t = 9.2, *df* 87, P < 0.001). The isotope ratios of black-browed albatrosses (Fig. 3, δ^{13}C: t = 2.2, *df* 20, P = 0.036; δ^{15}N: t = 2.4, *df* 20, P = 0.026), white-chinned petrels (Fig. 3, δ^{13}C: t = 3.2, *df* 6, P = 0.019; δ^{15}N: t = 2.9, *df* 6, P = 0.029) and rockhopper penguin chick feathers did not differ statistically from those of adults (δ^{13}C: t = 1.6 *df* 9, P = 0.155; δ^{15}N: t = 1.0 *df* 9, P = 0.338).

The calculated TLs of adult seabirds ranged over 1.3 TL (from 3.1 for dolphin gulls to 4.4 for white-chinned petrels, Table 1). Compared to seabird communities studied earlier (Table 2), the mean TL of 3.7 of the seabird community on New Island (excluding thin-billed prions, see Discussion) was at the lower end of the mean value range (3.5–4.5), but not significantly different, from other seabird communities. Seabirds at New Island had a range of 1.3 TL, compared to a range of 0.4 to 1.5 as reported in other seabird communities (Table 2).

Discussion

We use stable isotope signatures of seabirds breeding on New Island to compare their trophic position and distribution during foraging. The stable isotope signatures indicated a range of trophic positions, from low levels in scavenging dolphin gulls and in rockhopper penguins to high levels, especially in black-browed albatross and white-chinned petrels (Fig. 4).

Table 2 Trophic studies of seabird colonies

Mean TL	Min	Max	Range	n	Tukey	Reference
3.6	3.1	4.4	1.3	7	a, b, c	This study
4.1	4.0	4.5	0.5	5	a, c	Hobson and Welch (1992)
3.6	3.4	3.9	0.6	6[a]	a, b	Hobson et al. (1994)
3.5	3.0	4.4	1.5	19[b]	b	Hobson et al. (1994)
4.0	3.4	4.4	1.0	7	a, b, c	Sydeman et al. (1997)
3.8	3.1	4.5	1.4	7	a, b, c	Hobson et al. (2002)
4.1	3.4	4.6	1.2	15	c	Forero et al. (2004)
3.6	3.2	4.2	1.0	12	a, b	Rau et al. (1992)
3.8	3.4	4.0	0.6	6[c]	a, b, c	Thompson et al. (1999)
3.6	3.4	3.8	0.4	6[d]	a, b, c	Thompson et al. (1999)

Note that TLs were recalculated from the published δ^{15}N values, therefore they differ slightly from the TLs published in the original study. The study sites, tissues and reference species were as follows: Barrow Strait-Lancaster Sound, Canada; pectoral muscle; POM (TL = 1, δ^{15}N = 5.4‰) (Hobson and Welch 1992). For the comparison, only adult birds from the present study were considered, thin-billed prions were omitted, because calculated TL for this species possibly underestimated the real TL (see "Discussion"). Mean trophic levels that were not statistically different according to Tukey post hoc tests (homogenous subsets) are marked with a common letter

[a] Barkley Sound, Vancouver Island, Canada; pectoral muscle; POM (TL = 1, δ^{15}N = 6.8‰) (Hobson et al. 1994)

[b] Northern Gulf of Alaska; pectoral muscle, euphausids (TL = 2.5, δ^{15}N = 11.2‰) (Hobson et al. 1994), Gulf of the Farallones, California, USA; egg albumen; euphausids (TL = 2.5, δ^{15}N = 11.2‰) (Sydeman et al. 1997), North Water Polynya, Canada; pectoral muscle; *Calanus hyperboreus* (TL = 2, δ^{15}N = 7.9‰) (Hobson et al. 2002), coast of Chubut province, Argentina, whole blood, *Engraulis anchoita* (TL = 3.2, δ^{15}N = 16.4‰) (Forero et al. 2004), Weddell Sea, pectoral muscle, *Euphausia superba* (TL = 2.2, δ^{15}N = 2.3‰) (Rau et al. 1992)

[c] Northern Iceland, liver, *Mallotus villosus* (TL = 3.2, δ^{15}N = 10.8‰) (Thompson et al. 1999)

[d] Southern Iceland, liver, *Mallotus villosus* (TL = 3.2, δ^{15}N = 10.8‰) (Thompson et al. 1999)

Penguins

Penguin feathers are grown shortly after the breeding season, when the penguins come back to perform a complete moult on land. Before the moult, they feed to replenish their body reserves, and the moulted feathers will mainly reflect the diet and foraging range during these feeding trips, in late summer. During this time, the birds are not bound to the colony, as the chicks have fledged, and little is known about their diet and distribution during this time.

The mean δ^{13}C values in the three species of penguins were slightly greater than those of squid- and fish-samples, suggesting that they were foraging in waters around the Falkland Islands. Gentoo penguins had a very small range of δ^{13}C values, while there was a much larger range in Magellanic penguins and rockhopper penguins, suggesting

that in these species, individuals may choose different foraging areas.

Rockhopper penguins had lower δ^{15}N values than Magellanic penguins and gentoo penguins (Fig. 2). The stable isotope values are consistent with studies on diet composition and feeding ranges of the three species at New Island (Thompson 1989; Pütz et al. 2001; Boersma et al. 2002). These characterise gentoo penguins as a mainly fish-feeding species in inshore waters (highest δ^{13}C and δ^{15}N values), Magellanic penguins as feeding mainly on squids at an intermediate distance to the shore (<100 km) (intermediate δ^{15}N values) and rockhopper penguins as feeding mainly on crustaceans either near the shore or far from the colonies (>100 km) (lowest δ^{15}N values). The stable isotope data suggest a substantial overlap in feeding areas between all three species and in TL between gentoo penguins and Magellanic penguins. Conventional diet analyses suggest a high flexibility of diet, as well as possible seasonal changes in all three species (Table 3). This is only reflected in δ^{15}N values of rockhopper penguin and Magellanic penguins, which show large variation, while values of gentoo penguins indicate little variation in diet at least during the pre-moult foraging trips. With a larger sample size, it would be useful to explore interannual differences in diet and foraging areas during the pre-moult foraging trips.

The TLs calculated for gentoo penguins at New Island are similar to those from South Georgia and the South Shetland Islands (Table 4), which is surprising because a diet analysis at South Georgia suggested that a higher proportion of crustaceans was consumed in southern waters (Croxall et al. 1997). No diet information is available for the Kerguelen population, but calculated TL suggests fish to be even more important in this population. However, the high values we obtained from Kerguelen samples (Table 4) are probably an overestimation of the real TL. The higher of the two δ^{15}N values (Table 4) is from a colony that feeds in an enclosed bay (Cherel and Hobson 2007), which may have not been represented by the δ^{15}N value in POM that was used as a baseline for the Kerguelen Islands (Altabet and Francois 1994).

Magellanic penguins breeding at New Island fed at a lower TL than on the coast of Argentina (Table 4). At New Island, small squids rather than fish were the most important prey (Thompson 1989). The high variation of both carbon and nitrogen isotope ratios observed for Magellanic penguins in this study, indicated individual differences and widely scattered feeding areas during the pre-moult period. Individual and sex-dependent differences in diet as reported for the Patagonia population may also be responsible for the high variation (Forero et al. 2002a).

Crustaceans dominated the diet of rockhopper penguins in the Falkland Islands, Crozet Island and the Kerguelen Islands (Thompson 1989, Tremblay and Cherel 2003). This

Table 3 Diet composition of the focal species from published papers and reports

Species	Season	Locations	n	Fish (%)	Squid (%)	Crust (%)	Reference
GEPE	Oct–Dec 1986	NI	16	21.5	39.4	39.1	Thompson (1989)
GEPE	Dec–Feb 1986/1987	NI	27	34.3	9.3	56.4	Thompson (1989)
GEPE	Nov 1987	KI	10	25.8	24.5	49.7	Thompson (1989)
GEPE	1986–2000	FI	252	55.0	10.0	35.0	Clausen and Pütz (2002)
GEPE	Feb 1986	SG	40	30.0	0.0	70.0	Croxall et al. (1997)
ROPE	Nov–Dec 1986	NI	31	0.6	38.9	60.6	Thompson (1989)
ROPE	Dec–Feb 1986/1987	NI	32	2.2	46.4	51.4	Thompson (1989)
ROPE	Mar 1987	NI	13	14.4	78.0	7.6	Thompson (1989)
ROPE	1986–2000	FI	187	25.0	25.0	50.0	Clausen and Pütz (2002)
ROPE	Oct–Nov 1996	AI	34	12.2	43.9	43.7	Tremblay and Cherel (2003)
ROPE	Jan–Feb 1998–1999	KI	36	2.9	0.0	97.1	Tremblay and Cherel (2003)
ROPE	Jan–Feb 1998–1999	CI	27	4.3	0.6	95.1	Tremblay and Cherel (2003)
MAPE	Oct–Dec 1986	NI	12	12.4	84.1	3.5	Thompson (1989)
MAPE	Dec–Feb 1986/87	NI	39	40.0	31.0	29.0	Thompson (1989)
MAPE	Nov–Dec 1987	KI	6	78.2	15.6	6.2	Thompson (1989)
MAPE	1986–2000	FI	282	40.0	40.0	20.0	Clausen and Pütz (2002)
BBAL	Jan–Apr 1987	NI	32	68.1	3.6	23.1	Thompson (1989)
BBAL	Jan 1988	SJ	20	50.9	39.6	4.4	Thompson (1989)
BBAL	Feb–Mar 1975–1978	SG	138	38.0	20.6	39.9	Prince (1980)
BBAL	Feb–Apr 1994–1995	KI	114	73.1	9.7	<0.1	Cherel et al. (2000b)
WCPE	All months 1984/85	BC	102	75.4	11.4	13.2	Jackson (1988)
WCPE	Feb 1986	SG	45	16.0	25.0	59.0	Croxall et al. (1995)
TBPR	Jan–Feb 1987	NI	37	2.2	14.9	82.9	Thompson (1989)
TBPR	1994/1995–1996/1997	KI	85	5.7	2.9	91.3	Cherel et al. (2002)
IMCO	Oct–Dec 1986	NI	25	18.5	11.5	70.0	Thompson (1989)
IMCO	Dec–Feb 1986/1987	NI	33	89.4	0.5	10.1	Thompson (1989)

All percentage values refer to the part of the fresh mass that could be classified in one of the groups. Species abbreviations as in Table 2

NI New Island (Falkland Islands), *KI* Keppel Island (Falkland Islands), *FI* Falkland Islands, *SG* South Georgia, *AI* Amsterdam Island, *CI* Crozet Island, *SJ* Steeple Jason (Falkland Islands), *BC* Benguela Current

agrees with the calculated TL for the New Island population, while the TL calculated for birds from the Kerguelen Islands and Crozet Island apparently overestimates the real TL (Table 4). The TL calculated for the population from Amsterdam Island appears too low. The chosen reference value (Altabet and Francois 1994) is apparently not representative for this island. Diet analysis suggests a higher rather than a lower TL for this population (Tremblay and Cherel 2003).

Thin-billed prion

In comparison with the other species, thin-billed prions forage much further south, as indicated by strongly depleted ^{13}C. Thin-billed prions use long and short foraging trips of up to 8 days during the breeding period (Quillfeldt et al. 2007b). During long trips, they reach the waters south of the Antarctic Convergence where foodwebs will have a lower $\delta^{15}N$ and $\delta^{13}C$ baseline value (Altabet

and Francois 1994; Best and Schell 1996). The wide scatter of values from thin-billed prion feathers may reflect individuals moulting in areas north and south of the Antarctic Convergence (e.g., Quillfeldt et al. 2008a). As the actual foraging areas of the prions were unknown, and potentially encompass a wide geographic distribution, we could not assign a baseline nitrogen value for this species, and we could not calculate the trophic level of individuals.

White-chinned petrel

Successfully breeding white-chinned petrels moult during the non-breeding season. This species appears to be highly flexible in their diet according to the literature. In the Benguela Current the species was mainly piscivorous (Jackson 1988) and in South Georgia *Euphausia superba* was the most important prey (Table 3, Croxall et al. 1997). The high TL calculated for the New Island population indicated a high percentage of fish in the diet, consistent

Table 4 Stable isotope ratios from previous studies

Species	Age	Seas.	Tissue	δ^{13}C (‰)	δ^{15}N (‰)	TL	References
GEPE[a]	Chick	B	Feather	−23.5	7.6	3.65	Quillfeldt et al. (2005)
GEPE[b]	Adult male	B	Blood (cells)	−18.8	9.1	3.89	Bearhop et al. (2006)
GEPE[b]	Adult female	B	Blood (cells)	−18.9	8.6	3.74	Bearhop et al. (2006)
GEPE[c]	Chick	B	Blood (whole)	−18.2	11.0	4.97	Cherel and Hobson (2007)
GEPE[c]	Chick	B	Blood (whole)	−15.9	12.9	5.53	Cherel and Hobson (2007)
ROPE[d]	Chick	B	Blood (whole)	−19.5	9.2	1.79	Cherel and Hobson (2007)
ROPE[e]	Chick	B	Blood (whole)	−21.2	6.8	3.44	Cherel et al. (2007)
ROPE[e]	Adult	B	Blood (whole)	−20.9	7.5	3.65	Cherel et al. (2007)
ROPE[e]	Adult	NB	Blood (whole)	−19.7	7.6		Cherel et al. (2007)
ROPE[c]	Chick	B	Blood (whole)	−20.8	8.1	4.12	Cherel and Hobson (2007)
MAPE[f]	Adult	B	Blood (cells)	−16.7	18.8	4.05	Forero et al. (2004)
MAPE[f]	Adult male	B	Blood (whole)	−16.2	18.9	4.08	Forero et al. (2004)
MAPE[f]	Adult female	B	Blood (whole)	−16.5	18.8	4.05	Forero et al. (2004)
MAPE[f]	Chick	B	Blood (whole)	−16.6	19.1	4.14	Forero et al. (2002a)
BBAL[c]	Chick	B	Feather	−19.6	12.4	5.06	Cherel et al. (2000)
BBAL[c]	Adult	NB	Feather	−17.6	15.4		Cherel et al. (2000)
BBAL[b]	Adult	NB	Feather	−14.9	15.9		Phillips et al. (2007)
TBPR[c]	Chick	B	Feather	−22.7	8.9	4.35	Cherel et al. (2002)
TBPR[c]	Adult	NB	Feather	−24.3	8.5		Cherel et al. (2002)
WCPE[b]	Adult	NB	Feather	−15.5	17.5		Phillips et al. (2007)
IMCO[f]	Adult	B	Blood (cells)	−16.3	20.0	4.4	Forero et al. (2004)
DOGU[f]	Adult	B	Blood (cells)	−15.3	20.5	4.6	Forero et al. (2004)

Note that TLs were calculated from the published δ^{15}N values and were not taken from the original paper. TL were calculated by Eq. 2 with the reference values. NB in the season (seas.) column indicates isotope ratios from the non-breeding season during which the birds location is unknown and hence TL could not be calculated. Species abbreviations as in Table 1

[a] South Shetland 62°S, 58°W, *Euphausia superba,* TL = 2.3, δ^{15}N = 3.3‰ (Frazer 1996)

[b] South Georgia 54°S, 38°W, Euphausids TL = 2.3, δ^{15}N = 4.2‰ (Wada et al. 1987)

[c] Kerguelen Islands, 49°S, 70°E, POM TL = 1, δ^{15}N = −2.0‰ (Altabet and Francois 1994)

[d] Amsterdam Island 38°S, 77°E, POM TL = 1, δ^{15}N = 7‰ (Altabet and Francois 1994)

[e] Crozet Island 46°S, 52°E, POM TL = 1, δ^{15}N = −1‰ (Altabet and Francois 1994)

[f] Chubut, Argentina, *Engraulis anchoita* TL = 3.2, δ^{15}N = 16.4‰ (Forero et al. 2004)

with observations of the species to feed on discards from trawlers and bait from longliners on the Patagonian Shelf (Barton 2002). A comparison with the mean isotope values of prey classes also shows fish to be their most important prey. Both carbon and nitrogen isotope values from the South Georgia population (Table 3, Phillips et al. 2007) were remarkably similar to values of adult white-chinned petrels from New Island, suggesting that they both feed in the same area, which is most likely the Patagonian Shelf, during the non-breeding season. The importance of the Patagonian Shelf for the South Georgia population is well documented by satellite telemetry (Croxall and Wood 2002). The high percentage of crustaceans in the diet on South Georgia (Croxall et al. 1997) is not reflected in the δ^{15}N value of New Island adult feathers, while the down of white-chinned petrel chicks had non-significantly lower δ^{13}C and δ^{15}N values. Although not significant after

Bonferroni correction, this difference may indicate different feeding areas and a lower TL diet during the breeding season than during adult moult.

High δ^{13}C values, similar to those for the adult white-chinned petrels in this study, are found in areas of peak productivity (Francois et al. 1993). During the breeding season, the birds have to trade-off flight distance versus visiting the best feeding areas, whereas in non-breeding seasons they can stay in the most productive areas. This might explain the difference in carbon isotope values between adult feathers and chick down, a difference that is also found in nitrogen isotope values but to a lesser extent. The same pattern is also found in black-browed albatrosses, gentoo penguins and Magellanic penguins. However, as variation for POM isotope ratios were unknown, a seasonal effect reflecting changes in POM carbon isotope values cannot be excluded.

Black-browed albatross

The calculated TL for adult black-browed albatrosses is the second highest of the study (Table 1); this result is supported by conventional diet studies in the Falkland Islands and by a comparison with the mean isotope values of prey classes. Fish was the most important prey in those studies (Thompson 1989) and even more important in the Kerguelen Islands (Cherel et al. 2000b). This is also reflected in the calculated TL that was higher in the latter island group (Table 4). Black-browed albatrosses are also known to feed on discards from trawlers (White 1999) and suffer most of all seabirds breeding on New Island from mortalities due to long-line fishing (Barton 2002). At South Georgia, crustaceans comprise a greater proportion of the diet than on New Island (Prince 1980; Thompson 1989). However, as for the white-chinned petrel, this observation was not reflected in the isotope values, and this population may also spend the non-breeding season on the Patagonian Shelf, as indicated by carbon isotope values (Table 4, Phillips et al. 2007) and satellite studies (Croxall and Wood 2002). Our results suggest that black-browed albatrosses and white-chinned petrels show much overlap both in feeding area and diet.

Imperial cormorant

The New Island population of the imperial cormorant has been found to feed mainly on fish, especially of the genus *Patagonotothen*, and crustaceans, especially *Munida gregaria* (Thompson 1989). The calculated TL indicates that fish may be more important during moult (Fig. 2). On the coast of Argentina the species seems to feed at a higher TL (Table 4, Forero et al. 2004). The high $\delta^{13}C$ value found in the feathers of imperial cormorants indicates that the species mainly feeds in coastal waters, consistent with ship-based surveys in the Falkland Islands (White 1999). A high $\delta^{13}C$ value is also consistent with less pelagic and more inshore feeding grounds or benthic prey (Hobson et al. 1994).

Dolphin gull

Dolphin gulls moult during the non-breeding season, and very little is known about their behaviour in the winter period. In summer, the species is a specialised scavenger, feeding on southern sea lion *Otaria flavescens* excrement and scavenged prey items in colonies of Magellanic penguins and imperial cormorants, and less importantly, on invertebrates in the intertidal zone (Yorio et al. 1996). The low TL indicated by our studies suggests that invertebrates are important in this gull's diet. These may be derived either from scavenging on the faeces sea lions that are depleted in ^{15}N or from foraging in the intertidal zone (Yorio et al. 1996).

Seabird community studies

The range of TLs in the seabird communities compared in this study is remarkably similar (Table 2). While there is certainly an effect of species number on the range of TL, all values were in the range 2.8–4.6 and mean values varied only by 0.6 TL. The seabird community breeding on New Island had a mean TL at the lower end of the range and significantly lower than the mean value in Patagonia (Table 2). Seabirds in coastal Argentina rely heavily on the abundant small fish *Engraulis anchoita* while for the birds on New Island crustaceans and small squid are more important (Thompson 1989). The seabird community of New Island may therefore be less vulnerable to direct effects of overfishing than colonies on the coast of Patagonia, and the removal of fish from the ecosystem may even increase the abundance of crustaceans (Lampert and Sommer 1993).

Stable isotope analysis, as applied in most ecological studies, has to deal with the problem of providing only two tracers ($\delta^{13}C$, $\delta^{15}N$) in a system with more than two variables (Cherel and Hobson 2007). The large feeding ranges of many seabirds are particularly challenging. Both $\delta^{13}C$ and $\delta^{15}N$ show large spatial variation that is especially notable near the various frontal systems in the southern hemisphere. Getting good estimates of a species TL can be impossible when it feeds in more than one water mass, as demonstrated by the results obtained from thin-billed prions in the present study. This will be true so long as our knowledge of the spatial and temporal variation of stable isotopes in the ocean remains patchy.

The present study provides baseline carbon and nitrogen stable isotope information for a range of pelagic and coastal seabird species at New Island, collected non-invasively. It demonstrates that the carbon and nitrogen stable isotope values are in good agreement with data from conventional diet analyses, and can be used as a starting point for long-term, non-invasive monitoring.

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