Resource partitioning within a tropical seabird community: new information from stable isotopes

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ABSTRACT: Characteristics of the tropical oceanic environment (low productivity, little seasonality) and poor diversity of tropical seabird foraging methods and prey relative to temperate and polar species suggest that tropical seabirds overall encompass a narrow range of isotopic niches, with large overlaps among species. To test this hypothesis, we examined the stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic composition of blood and feathers of 5 seabird species from Europa Island, Mozambique Channel. While differences were small, blood δ^{13}C and δ^{15}N values characterized 5 distinct and non-overlapping trophic niches during the breeding period. Seabirds used 2 distinct foraging areas (δ^{13}C), one used by sooty tern *Sterna fuscata* and white-tailed tropicbird *Phaethon lepturus* and one used by red-footed booby *Sula sula* and great *Fregata minor* and lesser *F. ariel* frigatebirds. Seabird species overall encompassed less than 1 trophic level (δ^{15}N), which is in agreement with a diet mainly based on flying fish and squid. Feather δ^{13}C and δ^{15}N values showed that the trophic structure of the community was different during the breeding and non-breeding (moulting) periods, suggesting a shift in the feeding ecology when adult birds were no longer central-place foragers. The stable isotope method underlined sex-related (red-footed booby) and age-related (great frigatebird immatures and adults) feeding strategies. It also suggested that breeding adults could feed themselves on different prey than those given to their chicks (sooty tern). Within the tropical pelagic ecosystem, seabirds overall shared the same trophic level as large predatory fishes (albacore, yellowfin and skipjack tunas), but they had lower δ^{15}N values than the deeper-dwelling bigeye tuna and swordfish. We conclude that analyzing stable isotope values in blood and feathers appears to be a promising alternative method for investigating food and feeding ecology of tropical seabirds year round, and for determining sex- and age-related differences in their foraging strategies. A limitation of the method is the lack of information on marine isoscapes; future studies aimed at isotopically characterizing the tropical marine environment could help to associate consumer signatures to geographic origins.

KEY WORDS: Booby · Frigatebird · Pelagic ecosystem · Sooty tern · Tuna · Trophic segregation

INTRODUCTION

The way in which food and space are allocated plays a pivotal role in the structuring of animal communities. Accordingly, the mechanisms by which species of seabirds are segregated usually involve some combination of diet, feeding range and area, and feeding methods and behaviour (Ashmole 1971, Ainley et al. 1990, Croxall et al. 1997). Most of these previous studies were land-based and thus focused more on dietary segregation than on space utilization, and more on the chick-rearing period than on the whole cycle (Ashmole & Ashmole 1967, Harrison et al. 1983, Ridoux 1994). More recently, our knowledge of the foraging ecology

of breeding seabirds in relation to the marine environment (at least for larger species) increased considerably due to the development of animal-attached electronic devices (Ropert-Coudert & Wilson 2005). However, several limitations (including the size of the devices and their cost) preclude their use at the scale of a whole community on a given season or year, and, until recently, during the non-breeding period (Croxall et al. 2005).

Complementary to conventional dietary methods and bio-logging, stable isotope analysis has been increasingly applied to a number of investigations on diet, trophic relationships and foraging zones of seabirds (Hobson et al. 1994, Thompson et al. 1995, Cherel et al. 2000). This approach is based on the fact that the ratios of the stable isotopes of nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) and carbon ($^{13}C/^{12}C$, $\delta^{13}C$) in predator proteins reflect those in prey species in a predictable manner. Consumer tissues are enriched in ^{15}N relative to their food; consequently, $\delta^{15}N$ measurements serve as indicators of a consumer trophic position (Vanderklift & Ponsard 2003). In contrast, $\delta^{13}C$ values vary little along the food chain and are mainly used to determine primary production sources in a trophic network (Kelly 2000). In the marine environment, $\delta^{13}C$ values indicate consumer foraging areas, i.e. inshore versus offshore, pelagic versus benthic, or latitudinal variations in the contribution to food intake (Hobson et al. 1994, Cherel & Hobson 2007).

Depending on tissue-specific isotopic turnover, stable isotope measurements reflect average dietary records over days to years and thus have the potential to resolve nutritional change at different time scales (Dalerum & Angerbjörn 2005). In avian studies, whole blood and feathers are the most commonly targeted tissues, because they can be sampled easily and nondestructively in the field. Due to different turnover times, they integrate different periods of information. Whole blood represents a period of days to weeks, depending on bird size, whereas feathers reflect the diet at the time they were grown because keratin is inert after synthesis (Hobson & Clark 1992, 1993, Bearhop et al. 2002). Since the annual cycle of many seabirds typically includes a complete moult starting after reproduction, feathers and whole blood collected during the breeding period therefore reflect the isotopic signature during the previous moulting (non-breeding) period and the breeding period itself, respectively. Moreover, whole blood and feathers can be collected from a relatively large number of individuals and species during the same sampling season, thus potentially allowing the study of overall trophic structure of seabird communities over the annual cycle.

Community-based investigations of seabird diet and feeding ecology using stable isotopes have been conducted during the breeding period in temperate and polar waters (Hobson et al. 1994, Thompson et al. 1999, Sydeman et al. 1997, Forero et al. 2004). To our knowledge, however, no comparable information is available either on tropical species (except albatrosses, Finkelstein et al. 2006, Awkerman et al. 2007) or over the non-breeding period. The primary goal of the present study was therefore to measure the isotopic niche (Newsome et al. 2007) of tropical seabirds and to use this tool to investigate the trophic structure of their community on an oceanic island. Tropical marine systems are characterized by low productivity and little seasonality relative to non-tropical systems. Oligotrophic tropical waters therefore sustain a relatively low density and biomass of seabirds (Ainley & Boekelheide 1983), including Procellariiforms (petrels and shearwaters), Pelecaniforms (boobies, frigatebirds and tropicbirds) and Charadriiforms (terns and noddies). Most of these species forage in multispecies flocks and are confined to feed near or above the water surface where they mainly prey upon 2 groups of epipelagic organisms, flying fish (Exocoetidae) and flying squid (Ommastrephidae) (Ashmole & Ashmole 1967, Harrison et al. 1983, Ballance & Pitman 1999). Taking into account the marine environment and relatively poor diversity of seabird foraging methods and prey, we predicted that the stable isotope signatures of tropical seabirds overall would encompass a narrow range in $\delta^{13}C$ and $\delta^{15}N$ values, with large overlaps among species. Using the isotopic signature of whole blood and feathers, the trophic structure of the community was moreover compared during the breeding and poorly known non-breeding periods. We also looked at possible sex-related and age-related differences in the feeding ecology of tropical seabirds by comparing the $\delta^{13}C$ and $\delta^{15}N$ values of breeding males and females, as well as of immatures and chicks. Stable isotope analyses were also performed for seabird prey to create a basis for the interpretation of the isotopic signatures of predators because the method is at its most powerful when combined with conventional approaches (Bearhop et al. 2004). Finally, the isotopic signatures of birds and their food were compared to those of large predatory fishes occurring in the area because the most important foraging strategy for tropical seabirds is to feed in association with subsurface predators, primarily tunas (Ballance & Pitman 1999).

MATERIALS AND METHODS

This work was conducted as part of a larger investigation on the food and feeding ecology of the seabird community from Europa Island in austral winter (August and September 2003) in relation to the tropical

marine environment using complementary methodologies (observations at sea, dietary analysis, electronic devices and stable isotopes) (Weimerskirch et al. 2004, 2005a,b, 2006, Jaquemet et al. 2005, present study).

Study site and sample collection. Europa Island (22° 20′ S, 40° 21′ E) is a tropical coralline island located in the southern part of the Mozambique Channel, western Indian Ocean. In winter (June to October), the seabird community is composed of 6 species: sooty terns *Sterna fuscata* (about 3 000 000 individuals), white-tailed tropicbirds *Phaethon lepturus* (2000 birds), red-footed boobies *Sula sula* (9000 birds) and great *Fregata minor* and lesser *F. ariel* frigatebirds (3000 and 4000 birds, respectively), together with a smaller number of Audubon's shearwaters *Puffinus lherminieri* (<100 birds, Le Corre 2001). Since breeding is not synchronous, the 5 former seabirds were studied during the incubation and/or chick-rearing periods, depending on breeding phenology. Importantly, tissue samples were collected within a few wk (18 August to 30 September 2003), when sampled adults were all breeders (and were thus non-breeders in the preceding months).

The 4 pelecaniform species were sexed and aged by voice, plumage characteristics and/or molecular sexing (Lormée et al. 2000). Randomly chosen individuals were food-, blood- and feather-sampled. Stomach contents of sooty terns and red-footed boobies were obtained by collecting spontaneous regurgitations from adults and chicks, and those of great frigatebirds also included some food samples from immatures (i.e. young birds having a plumage different from the adult one). Blood was collected into a heparinized syringe by venipuncture in the wing. Seventy-percent ethanol was added to whole blood, because that method does not alter the isotopic composition of tissues (Hobson et al. 1997). The top 2 to 4 cm of 2 primary feathers were also collected and stored dry in plastic bags.

Food items were identified using taxonomic keys (Smith & Heemstra 1986) and our own reference collection. Some well-preserved fish and squid specimens were subsequently used to determine $\delta^{13}C$ and $\delta^{15}N$ values of seabird prey. The isotopic signature of predatory fishes (swordfish *Xiphias gladius*, albacore *Thunnus alalunga*, yellowfin *T. albacares*, bigeye *T. obesus* and skipjack *Katsuwonus pelamis* tunas) occurring in the area was measured on a few adult specimens caught during an oceanic cruise that took place in the Mozambique Channel during the study period in September 2003 (Jaquemet et al. 2005).

Stable isotope analysis and methodological considerations. Before isotopic analysis, whole blood and feathers of seabirds and muscle samples from cephalopod and fish were dried in an oven at 60°C. Feathers were cleaned of surface contaminants using a 2:1 chlo-roform:ether rinse and then cut into small fragments. Muscle samples were ground to a fine powder and muscle lipids were removed using cyclohexane. The low lipid content of whole blood does not typically necessitate lipid extraction (Cherel et al. 2005). While overall statistically different (Kruskal-Wallis, H = 192.64, p < 0.0001), all mean values of C:N mass ratio encompassed a narrow range (3.1 to 3.5, always < 4) (see Tables 1–3). Such low values indicate low lipid content, thus allowing accurate comparisons of $\delta^{13}C$ values among sample types and groups of animals.

Relative abundance of ^{13}C and ^{15}N were determined using an Isoprime (Micromass) continuous-flow isotope-ratio mass spectrometer. Results are presented in the usual δ notation relative to PDB and atmospheric N_2 (air) for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) during each autorun indicate measurement errors <0.15‰ and <0.20‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

The isotopic signature of consumers may be affected by various extrinsic and intrinsic processes. Firstly, diet-tissue discrimination factors ($\Delta^{15}N$ and $\Delta^{13}C$) vary with tissue type and species (Vanderklift & Ponsard 2003). However, in fish-eating seabirds little specific variation was found in blood $\Delta^{15}N$ values and in feather $\Delta^{15}N$ values (review in Cherel et al. 2005), thus allowing comparisons of the nitrogen signatures between species to investigate their respective trophic positions. We assumed that $\Delta^{15}N$ values were identical between chicks, immatures and adult birds because no experimental work tested the effect of growth per se on $\Delta^{15}N$ in birds and modeling suggests that growing endotherms should show the same $\delta^{15}N$ values as those of adults fed the same diet (Ponsard & Averbuch 1999). Secondly, isotopic signature is dependent of carbon and nitrogen turnover rates that are, in turn, dependent on tissue type and body size. Using allometric equations between body mass and carbon half-life in avian red blood cells (Carleton & Martinez del Rio 2005), half-lives in seabird blood was estimated to range from 14 d (sooty tern) to 23 d (great frigatebird), thus indicating that almost all carbon (93%, corresponding to 4 half-lives) was renewed within 55 to 92 d for all the species. Hence, the trophic structure of the community during breeding was investigated over the medium term, i.e. at the scales of the last 2 to 3 mo. It was impossible to know precisely when feathers were built up, but adult primaries were non-abraded, fully grown feathers, indicating they were synthesised during the weeks/months before breeding. Thirdly, different isotopic gradients in the marine environment can overlap, thus leading to misinterpretation of isotopic signatures of consumers (Cherel & Hobson 2007). In the present work, we are confident that the well-

known benthic/pelagic gradient in carbon sources was of little influence on seabird $\delta^{13}C$ values because Europa is an oceanic island devoid of peri-insular shelf, and both tracking and visual observations of birds have shown that they were true oceanic species foraging offshore (Weimerskirch et al. 2004, 2005a, Jaquemet et al. 2005).

Statistics. Values are means ± SD. Data were statistically analysed using SYSTAT 9 for WINDOWS.

RESULTS

Adult isotopic signatures during the breeding and moulting periods

During the breeding season, the 5 sympatric seabird species from Europa Island were segregated by their overall isotopic signatures (MANOVA, Wilks' lambda, $F_{8,114} = 32.71$, p < 0.0001) and, in univariate analysis, both $\delta^{13}C$ (ANOVA, $F_{4,58} = 36.35$, p < 0.0001) and $\delta^{15}N$

blood values ($F_{4,58} = 29.70$, p < 0.0001). Post hoc Tukey's HSD multiple comparison tests indicated that all $\delta^{13}C$ values were highly significantly different among species, except between the white-tailed tropicbird and the sooty tern, and between the lesser frigatebird and the red-footed booby (Table 1). Multiple comparison tests showed similar $\delta^{15}N$ values for the white-tailed tropicbird and lesser and great frigatebirds, all the other values being significantly different (statistics not shown) (Fig. 1).

During the non-breeding period, seabirds were again segregated by their isotopic signatures (MANOVA, Wilks' lambda, $F_{8,114} = 25.15$, p < 0.0001) and, in univariate analysis, both $\delta^{13}C$ (ANOVA, $F_{4,58} = 18.77$, p < 0.0001) and $\delta^{15}N$ feather values ($F_{4,58} = 43.19$, p < 0.0001). Multiple comparison tests indicated that the white-tailed tropicbird had a higher $\delta^{13}C$ value than the other species, and that the 2 species of frigatebirds and sooty tern had similar $\delta^{13}C$ values. The $\delta^{15}N$ value of great frigatebird segregated the species from the other seabirds, which had nitrogen signatures that were not statistically different (Fig. 1).

All the seabird trophic niches during either the breeding or moulting periods differed by at least 1 parameter ($\delta^{13}C$ and $\delta^{15}N$ values), except those of sooty tern and lesser frigatebird, which greatly overlapped during the moulting period. It is also noticeable that the overall stable isotopic signature of adult seabirds encompassed a larger range during the moulting than during the breeding period (1.2 and 0.6‰, and 2.9 and 1.2‰ for $\delta^{13}C$ and $\delta^{15}N$ values, respectively). Finally, perhaps the most interesting result is that the trophic structure of the community differed during the 2 periods. For example, the white-tailed tropicbird had a low $\delta^{13}C$ and the highest $\delta^{15}N$
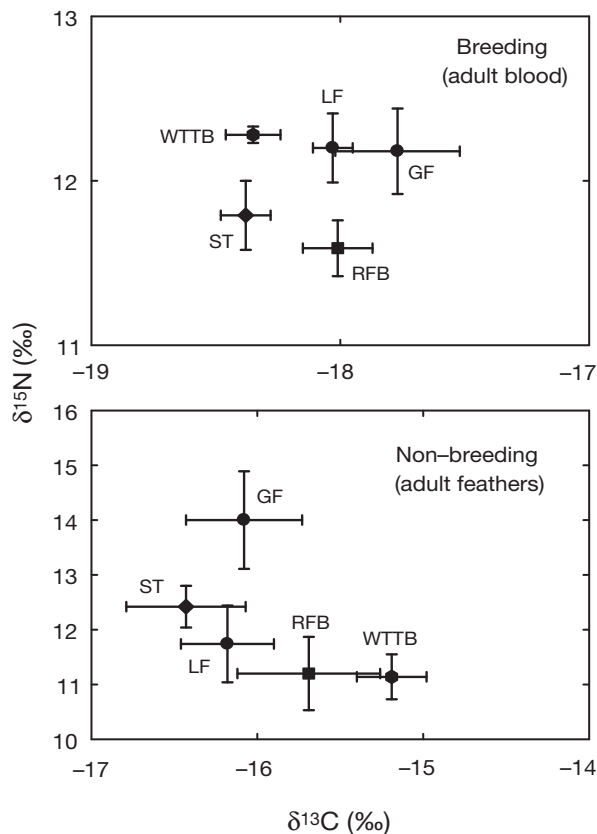

Fig. 1. Stable carbon and nitrogen isotope values of blood (upper panel) and feathers (lower panel) of adult seabirds from Europa Island. Values are means ± SD. Note that scales of both axes are different on upper and lower panels. GF: great frigatebird; LF: lesser frigatebird; RFB: red-footed booby; ST: sooty tern; WTTB: white-tailed tropicbird
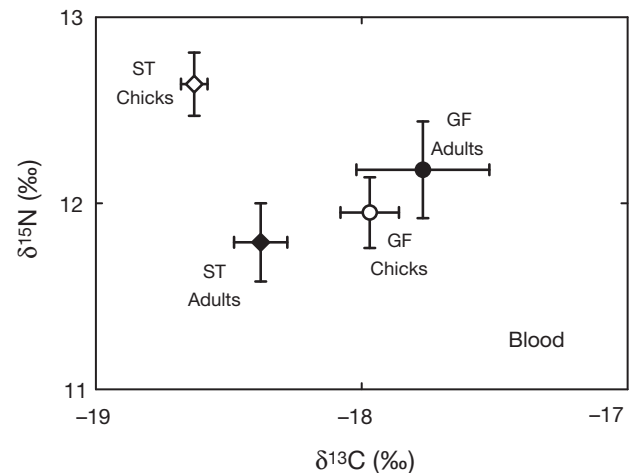

Fig. 2. Stable carbon and nitrogen isotope values of blood of adults and chicks of seabirds from Europa Island. Values are means ± SD. Abbreviations as in Fig. 1

value during the breeding period, while the species reached the highest δ^{13}C and lowest δ^{15}N value during the non-breeding period.

Sex- and age-related variations in δ^{13}C and δ^{15}N values

No statistically significant differences in tissue δ^{13}C and δ^{15}N values were found between adult and immature males and females of great frigatebird (statistics not shown). On the other hand, both blood and feather δ^{13}C values were higher in red-footed booby females than in males (blood and feathers: 2-sample t-tests, $t = 5.17$ and 2.72, p < 0.0001 and 0.014, respectively), while their δ^{15}N values were either marginally (blood: $t = 2.12$, p = 0.048) or not (feathers: $t = 0.21$, p = 0.840) statistically different (Table 2).

Adults and chicks of sooty tern segregated significantly by both their blood δ^{13}C and δ^{15}N values (2-sample t-tests, $t = 8.79$ and 12.65, respectively, both p < 0.0001) (Fig. 2). The 3 age classes of great frigatebird also segregated by their δ^{13}C and δ^{15}N values in blood (ANOVA, $F_{2,30} = 7.06$ and 5.35, p = 0.003 and 0.010, respectively) and feathers (ANOVA, $F_{2,30} = 28.27$ and 17.17, respectively, both p < 0.0001) (Fig. 3). The 3 main features were firstly that immatures and chicks had different blood δ^{13}C values, secondly that feather δ^{13}C values of adults and immatures significantly differed from that of chicks, and thirdly that adults had higher feather δ^{15}N values than chicks and immatures (Post hoc Tukey's HSD multiple comparison tests, all p < 0.003).

Seabird diet and δ^{13}C and δ^{15}N values of predators and prey

In winter 2003, birds from Europa Island fed mainly on fish and cephalopods, crustaceans being a minor component of their diet (Table 4). Red-footed boobies preyed more upon squids than sooty terns and great frigatebirds. However, ommastrephid squids (almost exclusively the purple-back flying squid *Sthenoteuthis oualaniensis*) were the main prey group eaten by these 3 seabird species (representing 16 to 50% of diet). The fish diet of sooty terns included a large diversity of species, the main family being nomeid fish. In contrast, the fish prey of red-footed boobies and great frigatebirds were restricted to 2 families, primarily flying fishes (Exocoetidae) and secondarily halfbeaks (Hemiramphidae).

Overall, seabirds, their prey and large predatory fish from the Mozam-

Table 1. Stable isotopic signature and C:N mass ratio of whole blood and feathers of seabirds from Europa Island. Values are means ± SD

Species and age classes	n	Tissue	δ^{13}C (‰)	δ^{15}N (‰)	C:N mass ratio
Sooty tern					
Adults	18	Blood	−18.38 ± 0.10	11.79 ± 0.21	3.43 ± 0.03
		Feathers	−16.43 ± 0.36	12.42 ± 0.38	3.24 ± 0.06
Chicks	15	Blood	−18.63 ± 0.05	12.64 ± 0.17	3.46 ± 0.04
		Feathers	−16.57 ± 0.18	13.68 ± 0.27	3.16 ± 0.02
White-tailed tropicbird					
Adults	7	Blood	−18.35 ± 0.11	12.28 ± 0.05	3.41 ± 0.05
		Feathers	−15.19 ± 0.21	11.14 ± 0.41	3.12 ± 0.01
Chicks	2	Blood	−18.56 ± 0.14	11.97 ± 0.24	3.44 ± 0.04
		Feathers	−16.26 ± 0.02	13.22 ± 0.01	3.10 ± 0.01
Red-footed booby					
Adults	21	Blood	−18.01 ± 0.14	11.59 ± 0.17	3.32 ± 0.04
		Feathers	−15.69 ± 0.43	11.20 ± 0.67	3.18 ± 0.03
Great frigatebird					
Adults	12	Blood	−17.77 ± 0.25	12.18 ± 0.26	3.35 ± 0.09
		Feathers	−16.08 ± 0.35	14.00 ± 0.89	3.27 ± 0.03
Immatures	11	Blood	−17.70 ± 0.09	11.90 ± 0.18	3.38 ± 0.06
		Feathers	−16.41 ± 0.33	12.84 ± 0.62	3.28 ± 0.03
Chicks	10	Blood	−17.97 ± 0.11	11.95 ± 0.19	3.45 ± 0.03
		Feathers	−17.38 ± 0.55	12.37 ± 0.37	3.21 ± 0.21
Lesser frigatebird					
Adults	5	Blood	−18.03 ± 0.08	12.20 ± 0.21	3.39 ± 0.04
		Feathers	−16.18 ± 0.28	11.74 ± 0.70	3.29 ± 0.02

Table 2. Stable isotopic signature and C:N mass ratio of whole blood and feathers of males and females of the great frigatebird and red-footed booby from Europa Island. Values are means ± SD

| Species and sex	n	Tissue	δ^{13}C (‰)	δ^{15}N (‰)	C:N mass ratio
Great frigatebird					
Females	6	Blood	−17.81 ± 0.25	12.06 ± 0.11	3.39 ± 0.12
		Feathers	−15.99 ± 0.40	14.15 ± 1.17	3.27 ± 0.03
Males	6	Blood	−17.73 ± 0.26	12.29 ± 0.32	3.32 ± 0.02
		Feathers	−16.16 ± 0.29	13.85 ± 0.57	3.28 ± 0.04
Red-footed booby					
Females	10	Blood	−17.90 ± 0.10	11.51 ± 0.19	3.33 ± 0.03
		Feathers	−15.45 ± 0.23	11.23 ± 0.63	3.17 ± 0.04
Males	11	Blood	−18.10 ± 0.09	11.66 ± 0.12	3.31 ± 0.04
		Feathers	−15.90 ± 0.47	11.17 ± 0.74	3.19 ± 0.03
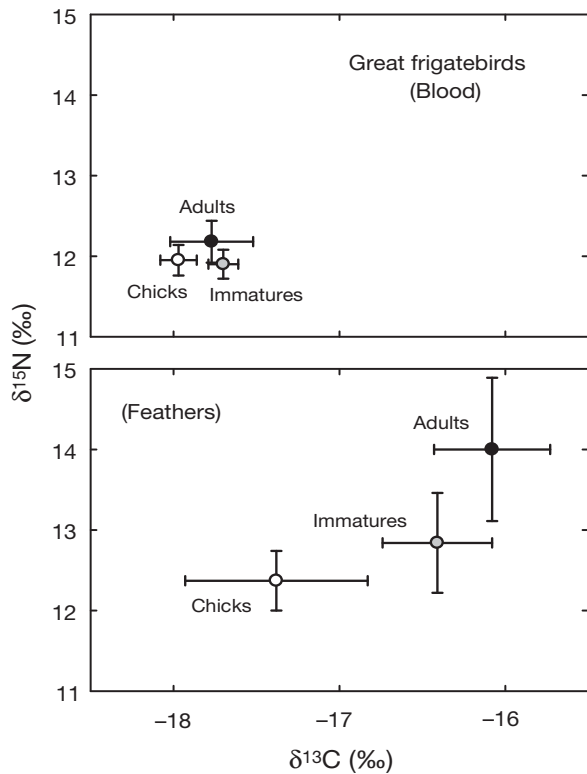
Fig. 3. Stable carbon and nitrogen isotope values of blood (upper panel) and feathers (lower panel) of adults, immatures and chicks of great frigatebirds from Europa Island. Values are means ± SD
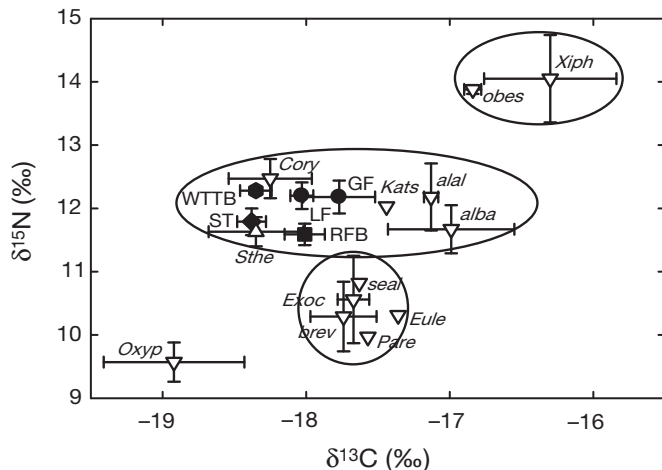

Fig. 4. Stable carbon and nitrogen isotope values of blood of adult seabirds (5 species) and of muscle of cephalopods (1 species) and fish (12 species) from Europa Island and the Mozambique Channel. Values are means ± SD. Abbreviations as in Fig. 1 for seabirds; *Sthe*: *Sthenoteuthis oualaniensis* (cephalopod); *alal*: *Thunnus alalunga*; *alba*: *T. albacares*; *brev*: *Prognichthys brevipinnis*; *Cory*: *Coryphaena* sp.; *Eule*: *Euleptorhamphus viridis*; *Exoc*: *Exocoetus monocirrhus*; *Kats*: *Katsuwonus pelamis*; *obes*: *T. obesus*; *Oxyp*: *Oxyporhamphus micropterus*; *Pare*: *Parexocoetus brachypterus*; *seal*: *Prognichthys sealei*; *Xiph*: *Xiphias gladius*

bique Channel were segregated in univariate analysis by both their $\delta^{13}C$ and $\delta^{15}N$ values (Kruskal-Wallis, $H = 113.83$ and 118.91, respectively, both p < 0.0001). $\delta^{13}C$ and $\delta^{15}N$ values ranged from -18.9 ± 0.5 to -16.3 ± 0.5‰, and from 9.6 ± 0.3 to 14.1 ± 0.7‰, for the half-beak *Oxyporhamphus micropterus* and swordfish, respectively (Table 3). Four groups of organisms can be clustered according to their isotopic signatures (Fig. 4): first *O. micropterus* alone, second a tight group including mainly the different species of flying fish, third a large group with a broad range in $\delta^{13}C$ values but a narrower range in $\delta^{15}N$ values that included albacore, yellowfin and skipjack tunas, the dolphin fish *Coryphaena* sp., purpleback squid and all the seabird species, and finally swordfish and bigeye tuna, which had the highest $\delta^{13}C$ and $\delta^{15}N$ values of the study.

DISCUSSION

Using the stable isotope method, this study presents 3 novelties when compared to the available information on seabird feeding ecology. First, it focuses on a community of tropical seabirds for which, except for albatrosses (Finkelstein et al. 2006, Awkerman et al. 2007), almost nothing is known about their $\delta^{13}C$ and $\delta^{15}N$ values. Second, while isotopic signature of several tissues (liver, muscle, bone) to infer seabird diet at different temporal scales was previously investigated (Hobson 1993), the present work is the first using $\delta^{13}C$ and $\delta^{15}N$ values of adult blood and feathers (Bearhop et al. 2000) to study trophic structure of a community during the breeding and non-breeding periods, respectively. Finally, we compared the trophic position ($\delta^{15}N$) of seabirds with that of other marine predators, an issue rarely investigated in the past (Hobson & Welch 1992).

Trophic structure of tropical and non-tropical seabird communities

As expected, the overall isotopic signature of the tropical seabird community from Europa Island during the breeding period encompassed narrower ranges in $\delta^{13}C$ and $\delta^{15}N$ values than those previously found in communities of temperate and polar seabirds (Hobson & Welch 1992, Hobson et al. 1994, Sydeman et al. 1997, Thompson et al. 1999, Forero et al. 2004). Such narrow ranges are probably linked to intrinsic characteristics of the tropical oceanic environment, underlining its spatio-temporal homogeneity (i.e. low productivity over large areas, little seasonality) and thus the smaller number of available oceanic foraging

Table 3. Stable isotopic signature and C:N mass ratio of muscle of seabird prey and of large predatory fishes caught in the vicinity of Europa Island. Values are means ± SD. ST: sooty tern; RFB: red-footed booby; GF: great frigatebird; LF: lesser frigatebird

Species	Source	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N mass ratio
Squid					
Ommastrephidae					
Sthenoteuthis oualaniensis	ST, RFB, GF, LF	31	−18.35 ± 0.33	11.63 ± 0.23	3.31 ± 0.12
Fish					
Hemiramphidae					
Euleptorhamphus viridis	RFB	1	−17.36	10.31	3.23
Oxyporhamphus micropterus	RFB	2	−18.92 ± 0.49	9.57 ± 0.31	3.20 ± 0.01
Exocoetidae					
Exocoetus monocirrhus	RFB, GF	4	−17.67 ± 0.11	10.56 ± 0.69	3.30 ± 0.03
Exocoetus sp.	RFB	2	−17.77 ± 0.30	9.38 ± 0.26	3.27 ± 0.02
Parexocoetus brachypterus	RFB	1	−17.57	9.97	3.21
Prognichthys brevipinnis	RFB	3	−17.74 ± 0.23	10.29 ± 0.55	3.26 ± 0.04
Prognichthys sealei	RFB	1	−17.63	10.82	3.22
Exocoetidae sp.	GF	2	−17.51 ± 0.13	10.07 ± 0.74	3.21 ± 0.02
All flying fishes	RFB, GF	13	−17.67 ± 0.17	10.22 ± 0.65	3.26 ± 0.04
Coryphaenidae					
Coryphaena sp.	GF	2	−18.25 ± 0.29	12.47 ± 0.31	3.27 ± 0.05
Scombridae					
Katsuwonus pelamis	Longlines	1	−17.44	12.03	3.24
Thunnus alalunga	Longlines	2	−17.13 ± 0.05	12.18 ± 0.53	3.15 ± 0.12
Thunnus albacares	Longlines	6	−16.99 ± 0.44	11.67 ± 0.38	3.11 ± 0.13
Thunnus obesus	Longlines	2	−16.84 ± 0.06	13.88 ± 0.07	3.21 ± 0.10
Xiphiidae					
Xiphias gladius	Longlines	16	−16.30 ± 0.46	14.05 ± 0.69	3.21 ± 0.19

habitats for tropical than non-tropical seabirds. Accordingly, the $\delta^{13}C$ values of large predatory fish from the tropical western Indian Ocean (where Europa Island is located) show little variation over a broad latitudinal zone (Ménard et al. 2007). Conversely, various water masses and fronts lead to strong gradients in $\delta^{13}C$ values of marine organisms from the southern Indian Ocean and, accordingly, to large differences in the $\delta^{13}C$ values (foraging areas) of subantarctic and Antarctic predators, including seabirds (Cherel & Hobson 2007, Cherel et al. 2007). Temperate and polar seabirds moreover include planktivorous and piscivorous species together with squid-eaters and apex predators-scavengers (Hobson et al. 1994, Ridoux 1994, Sydeman et al. 1997). In contrast, most of the tropical species prey upon fish and squid (Ashmole & Ashmole 1967, Diamond 1983, Harrison et al. 1983), thus restricting the range of $\delta^{15}N$ values (trophic levels) within their community. Finally, foraging methods of seabirds also differ between areas, with pursuit diving, and plunge diving and aerial feeding being mainly confined to cold and warm waters, respectively (Ainley & Boekelheide 1983).

Trophic structure of the seabird community during the breeding period

A main result of the present work is that, unlike our initial expectation, the bird isotopic signature indicated a well-defined trophic segregation within the community. While overall dif-

Table 4. Seabird diet (percentages by frequency of occurrence, FO, and by number, N) at Europa Island in August and September 2003

	Sooty tern		Red-footed booby		Great frigatebird	
	FO	N	FO	N	FO	N
No. of food samples	110		65		34	
No. of prey		659		296		172
Fish	**79**	**63**	**95**	**45**	**94**	**78**
Hemiramphidae	4	1	28	10	12	7
Exocoetidae	12	3	66	21	76	45
Mullidae	3	1	0	0	0	0
Carangidae	15	6	5	1	0	0
Nomeidae	41	28	0	0	0	0
Other families	11	11	3	1	21	6
Unidentified fish	26	13	31	12	41	20
Cephalopods	**86**	**36**	**62**	**55**	**41**	**19**
Ommastrephidae	81	34	55	50	35	16
Others	3	2	22	5	15	3
Crustaceans	**5**	**1**	**0**	**0**	**9**	**3**

ferences were small, blood $\delta^{13}C$ and $\delta^{15}N$ values characterized 5 distinct and non-overlapping isotopic niches—1 per species—during the breeding period. Blood $\delta^{13}C$ values indicated at least 2 foraging areas within the Europa community, one for sooty terns and white-tailed tropicbirds, and one for red-footed boobies and frigatebirds. Indeed, observations at sea showed that red-footed boobies and frigatebirds foraged in similar habitats, with frigatebirds favouring association with flocks of boobies (Jaquemet et al. 2005). Since red-footed boobies have a relatively limited foraging range (Weimerskirch et al. 2005a,b), their $\delta^{13}C$ values suggest that breeding frigatebirds mainly fed close to the island, with some individuals foraging over a much wider area (Weimerskirch et al. 2004, Jaquemet et al. 2005). During the study period, sooty terns and white-tailed tropicbirds occurred over all water masses surrounding Europa Island (Jaquemet et al. 2005) and their identical $\delta^{13}C$ values suggest foraging in similar habitats. However, they segregated through different feeding strategies, with sooty terns foraging in large flocks and white-tailed tropicbirds feeding in small flocks or solitarily (Ballance & Pitman 1999, Jaquemet et al. 2005, Spear & Ainley 2005).

Blood $\delta^{15}N$ values indicated that white-tailed tropicbirds and frigatebirds fed at a higher trophic level than sooty terns and red-footed boobies, the overall difference being less than a full trophic level. The diet of great frigatebirds at Europa was mainly composed of fish, primarily flying fish, and the difference between the isotopic signatures of flying fish and frigatebirds was consistent with the ^{15}N enrichment between fish muscle and seabird blood (Cherel et al. 2005). Our isotopic data therefore suggest that adults of both species of frigatebirds and of white-tailed tropicbirds preyed mainly upon flying fish, which is in general agreement with previous dietary investigations (Schreiber & Hensley 1976, Diamond 1983, Harrison et al. 1983, M. Le Corre et al. unpubl. data). When compared to other species, the lower $\delta^{15}N$ value of sooty terns can be explained by the smaller size of their prey, which included juvenile fish that had lower $\delta^{15}N$ values than flying fish and squid (S. Jaquemet et al. unpubl. data). Surprisingly, the nitrogen isotopic signature of red-footed boobies was similar to that of what is believed to be their main prey, the purpleback flying squid. The most likely explanation of that discrepancy is that boobies fed less upon squids and more on lower trophic-level organisms over the longer blood integration period than during the shorter collection period of dietary samples, which is in agreement with red-footed boobies preying more on flying fish elsewhere (Schreiber & Hensley 1976, Diamond 1983, Seki & Harrison 1989).

Seasonal changes in seabird community structure

A second main result of the present work is that the trophic structure of the community was different during the breeding and non-breeding periods. These seasonal changes contrast with isotopic data from a guild of subantarctic penguins and fur seals showing essentially the same trophic structure during summer and winter (Cherel et al. 2007). In both cases, however, variances in isotopic signatures were larger during the non-breeding period. This, together with the overall larger ranges in $\delta^{13}C$ and $\delta^{15}N$ values in feathers than in blood, supports our hypothesis that trophic niches widen when adult seabirds are no longer central-place foragers constrained by their terrestrial breeding sites (Cherel et al. 2007). Feather $\delta^{13}C$ and $\delta^{15}N$ values characterized 4 distinct trophic niches, with sooty terns and lesser frigatebirds having similar isotopic signatures. Comparison of seasonal $\delta^{13}C$ and $\delta^{15}N$ values within each species is blurred by tissue-dependent isotopic signatures due to metabolic routing. Feather (keratin) is significantly more ^{15}N-enriched (and often ^{13}C-enriched) than whole blood (Cherel et al. 2005), as underlined here by the differences in $\delta^{13}C$ and $\delta^{15}N$ values of chick feathers and blood that integrated the same temporal window. Nevertheless, taking these tissue-related differences into account, 2 main features emerge. (1) $\delta^{15}N$ values of white-tailed tropicbirds, red-footed boobies and lesser frigatebirds were lower during the non-breeding period, suggesting that seabirds fed more on lower trophic level organisms at that time. (2) $\delta^{13}C$ values of white-tailed tropicbirds were higher during the non-breeding period. This, together with $\delta^{15}N$ changes, indicates that the species fed in different habitats when moulting and breeding.

Sex- and age-related variations in seabird feeding ecology

In frigatebirds and boobies, females are larger than males and most hypotheses explaining the evolution of reversed sexual dimorphism assume size-related differences in feeding ecology (Weimerskirch et al. 2006). No isotopic differences were found in blood and feathers of the highly dimorphic great frigatebird. This does not preclude differences in provisioning strategy, kleptoparasitic behaviour and dietary habits of male and female frigatebirds (Lagarde et al. 2001, 2004, Congdon & Preker 2004), but suggests no major role of these differences in shaping the birds' trophic (isotopic) niches. On the other hand, $\delta^{13}C$ values of red-footed boobies were higher in females than in males, while their $\delta^{15}N$ values were similar, suggesting sex-related differences in foraging areas but not in diet. Accord-

ingly, breeding females range farther from Europa Island than males and both sexes feed on the same prey (Weimerskirch et al. 2006). Our data moreover suggest that these sex-related strategies occurred over the long-term, because identical isotopic results were found in both blood and feathers, corresponding to the breeding and non-breeding periods, respectively.

Also important, but rarely investigated (because food analysis is generally restricted to the diet of chicks), is the issue of the diet of adult seabirds when they feed for themselves (Pedrocchi et al. 1996). $\delta^{13}C$ and $\delta^{15}N$ values of blood of sooty tern chicks and adults differed significantly. This can be interpreted as adults feeding themselves on lower trophic level prey farther from the colony and capturing higher trophic level prey on their way back to the island for their chicks. Such trophic segregation between adults and chicks was previously found in Antarctic procellariiforms and Adélie penguins, with the higher trophic level of chicks being explained by adults provisioning offspring with higher-quality food to facilitate their growth (Hodum & Hobson 2000, Cherel 2008).

Finally, almost nothing is known about the food and feeding ecology of immature seabirds. Blood isotopic signatures of adults, immatures and chicks of great frigatebird were clustered with some subtle differences in their $\delta^{13}C$ values, suggesting that immatures used only a part of the adult foraging area during the breeding season. Feather isotopic signatures magnified the differences. Comparison of chick and adult values indicates that adult great frigatebirds foraged in different areas and preyed upon higher trophic level organisms during the non-breeding period. Interestingly, immature great frigatebirds had intermediary $\delta^{13}C$ and $\delta^{15}N$ values and segregated from adults by feeding at a lower trophic level, as previously found in the only seabird species so far investigated—the Magellanic penguin (Forero et al. 2002).

Seabirds as predators in the tropical pelagic ecosystem

Another main finding of the present work is that seabirds overall shared the same trophic level as albacore, yellowfin and skipjack tunas. The most likely explanation is that seabirds and fish fed upon the same prey. In the western Indian Ocean, seabirds commonly associate with feeding schools of skipjacks and to a lesser extent schools of yellowfin tunas and dolphinfish that force prey to the surface (Jaquemet et al. 2004). Food of skipjack and yellowfin tuna, however, shows large differences with that of seabirds (Roger 1994, Potier et al. 2007). Fewer squids and more crustaceans were eaten by tunas and the representation of the various fish families was different. This mismatch proba-

bly arose because some fish prey were caught in the deep, while others (flying fish and squid) were subject to avian predation while escaping from tunas (Ashmole & Ashmole 1967). Seabird prey isotopic signatures are in general agreement with tropical seabirds feeding mainly on flying fish. In contrast, the purpleback flying squid clustered with seabirds, its high $\delta^{15}N$ value suggesting that stomach content analysis overemphasized its trophic importance or that seabirds consumed squid together with more lower trophic-level organisms than previously recognized.

Seabirds are generally considered to be top predators, sharing a place at the apex of the food chain with marine mammals and some large pelagic fish, including sharks, tunas and billfishes. However, evidence from diet and stable isotopes indicates that this common paradigm is questionable. When compared to other predators, including those considered being generally from lower trophic levels (e.g. squid), there was significant overlap. Moreover, the most singular pattern to emerge from $\delta^{15}N$ values was that bigeye tuna and swordfish, not seabirds, were the highest top consumers in the western Indian Ocean. The 2 fish species are known to undertake extensive vertical migrations and to include large mesopelagic organisms in their diet (Bertrand et al. 2002, Ménard et al. 2007, Potier et al 2007), which is the likely explanation why $\delta^{15}N$ differences between these 2 species, seabirds and the more epipelagic tunas comprise almost 1 trophic level.

CONCLUSIONS

For seabirds, analyzing stable isotope values in whole blood and feathers appears to be a reliable method of investigating food and feeding ecology all year round. The method is at its most powerful when combined with other conventional (food analysis, at-sea survey) and non-conventional (bio-logging) approaches. It is probably best used to investigate community structure, seasonal- and age-related (immatures) trophic differences, and feeding habits of adult birds when they feed themselves.

A limitation of the method is the lack of detailed information on marine isoscape values, which could be used to further elucidate isotopic variation among consumers. Bio-logging and oceanography have recently pointed out the importance of various oceanographic features for foraging tropical seabirds (Weimerskirch et al. 2004, 2005a, Jaquemet et al. 2007). Future studies aimed at characterizing $\delta^{13}C$ and $\delta^{15}N$ gradients at various spatio-temporal scales are thus needed to shed light on seabird at-sea biology and thus on both natural and anthropogenic factors affecting their lives.

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