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Trophic ecology of marine birds and pelagic fishes from Reunion Island as determined by stable isotope analysis

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ABSTRACT: Stable nitrogen and carbon isotopes were used to investigate trophic ecology in tropical marine bird and fish communities from Reunion Island, western Indian Ocean. Firstly, isotope signatures in the liver of Barau's petrels *Pterodroma baraui*, Audubon's shearwaters *Puffinus lherminieri bailloni*, and white-tailed tropicbirds *Phaethon lepturus* were used to compare their trophic levels and determine whether they forage in the same areas while breeding on Reunion Island. Spatial and trophic segregations were noted among these seabirds. Barau's petrels seem to feed on prey of higher trophic levels than Audubon's shearwaters. Different isotopic signatures in adults and juveniles of these species suggest that these chick-rearing Procellariiformes adopt a dual food-provisioning strategy, making separate foraging trips to feed their fledglings and for their own maintenance. Satellite tracking should be undertaken to verify this hypothesis. Furthermore, novel data were obtained on the seabirds' interbreeding period by analyzing feather signatures. White-tailed tropicbirds are thought to change foraging areas during this season, although none of the birds seemed to shift diets. Secondly, isotopic signatures in the muscle of yellowfin tuna *Thunnus albacares*, skipjack tuna *Katsuwonus pelamis*, and common dolphinfish *Coryphaena hippurus* were used to gather information on their feeding behaviors in Reunion Island waters. Spatial and trophic segregations were also observed, particularly between common dolphinfish and the tuna species, where the former fed more on low trophic level coastal organisms under fish aggregating devices than did the latter. Finally, trophic interactions in bird and fish communities were investigated. Seabirds appear to be trophically more structured than fish, foraging in a wider range of areas. Our results confirmed feeding associations between Audubon's shearwaters and yellowfin tuna.

KEY WORDS: Feeding behavior · Seabirds · Tunas · Dolphinfish · Top predators · Western Indian Ocean · δ^{15}N · δ^{13}C

INTRODUCTION

Due to the importance of predator-prey relationships and their dynamics in the structure and evolution of animal communities, ecologists continuously focus on better understanding trophic interactions. Investigations of trophic interactions between seabirds and surface predating fish is currently a major objective of the study of top predators in the western Indian Ocean. Different methods such as stomach content analysis and satellite tracking have previously been used to this

end. An alternative and complementary approach to these methods is the measurement of naturally occurring stable isotopes in consumers and their prey. The principle underlying this approach is that stable isotope deviations of nitrogen and carbon in consumers reflect those of their prey as they are enriched in a predictable manner. Conventionally expressed as $\delta^{15}N$ (‰), the deviation of ^{15}N to ^{14}N generally exhibits a stepwise enrichment from 2 to 5‰ relative to dietary nitrogen (Kelly 2000). This discrepancy of $\delta^{15}N$ is caused by a selective retention of the heavy isotope and excretion of the light one. It provides a tool for comparing the relative trophic level of various consumers living in the same environment. The deviation of ^{13}C to ^{12}C (denoted as $\delta^{13}C$) is also enriched with respect to dietary carbon, but to a much lesser degree than $\delta^{15}N$, on the order of 1‰ (DeNiro & Epstein 1978). The most common use of $\delta^{13}C$ in marine ecological studies is as a spatial tracer. Relative reliance of primary consumers on coastal and/or benthic versus oceanic and/or pelagic primary production determines $\delta^{13}C$ values in food webs (France 1995), which can also vary among water masses in the open ocean (DeNiro & Epstein 1978, Francois et al. 1993). Stable isotope deviations also have the advantage of offering information on a larger time scale than stomach content analysis, which, although more precise in prey determination, only allows a very narrow insight into the animal's global trophic habits. Given that tissues have different isotopic turnover rates, $\delta^{15}N$ and $\delta^{13}C$ measurements of multiple tissues provide dietary information on different temporal scales.

Here we focused on 6 top predators belonging to the tropical seabird and pelagic fish communities of the marine ecosystem surrounding Reunion Island. Our knowledge of the local feeding behavior of 3 avian species, viz. Barau's petrel *Pterodroma baraui*, which is endemic to Reunion Island, Audubon's shearwater *Puffinus lherminieri bailloni*, and white-tailed tropicbird *Phaethon lepturus*, is limited to general information on foraging by adults (basic temporal habits, foraging techniques, and interspecific associations) obtained by sighting around Reunion Island and diet composition (percentages of squid versus fish prey) acquired from stomach contents of adults and chicks during the breeding period. The specific diet composition of these birds and their fledglings, their foraging areas during and outside of the breeding season, and the extent of associations among seabird species and between seabirds and pelagic fishes remain unknown. Three epipelagic fishes, viz. yellowfin tuna *Thunnus albacares*, skipjack tuna *Katsuwonus pelamis*, and common dolphinfish *Coryphaena hippurus*, are distributed worldwide and are thus more studied. Fairly detailed knowledge about their diets (species compositions and quantities) and foraging behaviors (e.g. geographical locations, depths, diurnal and seasonal cycles,

associations) has been acquired for these fishes from numerous studies conducted on populations from various locations in the world. Additional information specific to their feeding behaviors in the western Indian Ocean is needed, as these species are subject to increasing commercial fishing pressure in this area where data are still laking. These 3 fishes gather in Reunion Island waters in the austral summer (Roos et al. 2000). During this season, 6 species of seabirds breed on the island, including Barau's petrels, Audubon's shearwaters, and white-tailed tropicbirds (Barré et al. 1996). The combined study of these 2 communities is of much interest, as their foraging behaviors are closely linked (Jaquemet et al. 2004). Subsurface predators, such as tunas and dolphinfish, drive prey to the surface to facilitate their capture, thereby making these prey accessible to seabirds from the air. Using stable isotope analyses, we investigated and compared the trophic position and foraging range of each bird and fish species in light of data previously obtained by transects at sea and stomach content studies in an attempt to better understand the trophic position of each species, with respect to the others, when simultaneously present around Reunion Island.

MATERIALS AND METHODS

Sampling. The marine birds analyzed in this study were collected between 2001 and 2004 on Reunion Island (21°07'S, 55°33'E) situated 700 km east of Madagascar (Fig. 1). The sampling of chicks and adults took place during the breeding period from October to April for Barau's petrels and Audubon's shearwaters, and throughout the year for white-tailed tropicbirds. The fish were caught between January and May 2004 within 40 km of the Réunion Island coastline (Fig. 1).

Seabirds. The seabird community on Reunion Island comprises 6 species: Barau's petrel (3000 to 5000 pairs), Audubon's shearwater (5000 pairs), white-tailed tropicbird (2000 to 3000 pairs), brown noddy *Anous stolidus* (500 pairs), wedge-tailed shearwater *Puffinus pacificus* (several hundred pairs), and Mascarene black petrel *Pseudobulweria aterrima* (50 pairs at the most) (Bretagnolle et al. 2000, Le Corre et al. 2002, authors' unpubl. data). The species forming the most numerous colonies were sampled for this study. We collected 51 Barau's petrels, 59 Audubon's shearwaters, and 49 white-tailed tropicbirds on land following their collision with urban lights or from poaching seizures. Two age classes were determined (juvenile and adult) using characteristic features of the beak and the feathers (Barré et al. 1996, authors' unpubl. data). Only adults were sexed during dissection, as the gonads were not developed enough in fledglings

to differentiate males from females. The nutritional condition of each bird was also evaluated using the body condition index (BCI) proposed by Wenzel & Adelung (1996) that corresponds to the ratio of liver to kidney masses. BCI is significantly negatively correlated to the degree of emaciation, such that a smaller index indicates a more emaciated bird. The liver was removed and frozen at –20°C. Breast feathers were cut at their base and placed in plastic bags.

We chose to analyze $\delta^{13}C$ and $\delta^{15}N$ in the liver and feathers of birds, as these tissues reflect their dietary habits in different periods of their reproductive cycle. The feather provides a record of their diet during the time of its formation (Thompson & Furness 1995). Most seabirds molt at sea during the interbreeding season (Warham 1996). As such, the analysis of feathers collected on adults gives information on their dietary intake and foraging areas during the interbreeding season, whereas the analysis of feathers collected on juveniles is informative of their trophic ecology during the chick-rearing period. Furthermore, because carbon and nitrogen turnover rates are high in liver (2.6 d half-life for carbon in Japanese Quail; Hobson & Clark 1992ab), the isotopic deviation analysis in this tissue is an indicator of the trophic ecology of these seabirds at the time they were sampled, i.e. during their breeding season on Reunion Island.

Marine fishes. We sampled 20 yellowfin tuna, 40 skipjack tuna, and 45 common dolphinfish from sportfishing vessels. Many individuals were caught in the vicinities of fish aggregating devices (FADs) anchored within 23 km of Reunion Island, where these fish reside and feed while seasonally present in Reunion Island waters (Roos et al. 2000). Each fish was measured using the fork length (FL, from the tip of the snout to the fork of the caudal fin) and weighed when possible. Individuals were sexed during dissection by examination of the gonads. White muscle was sampled in the abdominal area above the vent of the fish and frozen at –20°C. In fish, we chose to analyze $\delta^{13}C$ and $\delta^{15}N$ in muscle because (1) it is the most commonly used tissue in trophic studies owing to the smaller amount of lipid and inorganic carbonates and to the low intrasample variability of $\delta^{13}C$ and $\delta^{15}N$ measurements (Sweeting et al. 2005), and (2) the isotopic turnover rate in this tissue (half-life around 50 d in yellowfin tuna, Graham unpubl. data) is likely to reflect fish diet in Reunion waters.

The nutritional and reproductive states of each animal were assessed, as they may affect $\delta^{13}C$ and/or $\delta^{15}N$ values (Doucett et al. 1999). The hepatosomatic index (HSI) served as an indicator of the individual's body condition:

$$\text{HSI} = (\text{liver weight/body weight}) \times 100 \qquad (1)$$

The gonadosomatic index (GSI) was calculated, as it is generally considered a useful measure of gonad maturation and spawning readiness and is based on the broad assumption that proportionally larger gonads indicate greater development (West 1990). GSI was calculated as follows:

$$\text{GSI} = (\text{gonad weight/body weight]} \times 100 \qquad (2)$$

Due to the limited data on the body weight of the sampled fish, this parameter was estimated from the length using weight–length relationships presented in Table 1.

Isotopic determination. To prepare for isotopic composition determination, bird liver and fish muscle were freeze-dried and ground to fine powder. As lipids are highly depleted in ^{13}C with regard to other af components due to fractionation occurring during lipid synthesis (DeNiro & Epstein 1977), isotopic analyses were performed on lipid-extracted samples. Lipid extraction was performed using 20 ml of cyclohexane on powder aliquots of about 1 g. An ultra Turax was used to homogenize the mixture (2×15 s). The sample was then centrifuged for 2 min at $804 \times g$. The supernatant containing lipids was discarded, whereas the pellet was dried on an aluminum plate at 60°C for 12 h. All utensils were washed with detergent, rinsed with tap water and deionized water (Milli-Q quality), followed by absolute ethanol, and dried in an oven at 60°C before use.

Pectoral feathers were washed vigorously in triple baths of 0.25 N sodium hydroxide solution alternated with triple baths of deionized water in order to remove adherent external contamination as well as the external lipidic layer resulting from preening. Feathers were then dried in an oven for 24 h at 50°C.

Stable carbon and nitrogen isotope assays were carried out on 1 ± 0.02 mg subsamples of powder loaded into tin cups. The ^{13}C, ^{12}C, ^{15}N, and ^{14}N abundances in the samples were determined using continuous-flow isotope-ratio mass spectrometry (CF-IRMS). Analyses were conducted using a Europa Scientific ANCA-NT 20-20 Stable Isotope Analyzer with ANCA-NT Solid/Liquid Preparation Module (Europa Scientific).The CF-IRMS was operated in the dual isotope mode, allowing $\delta^{15}N$ and $\delta^{13}C$ to be measured on the same sample. Every 10 samples were separated by 2 laboratory standards (leucine), which were calibrated against 'Europa flour' and IAEA

standards N1 and N2. Experimental precision (based on the standard deviation of replicate measurements of the internal standards) was 0.10‰ for $\delta^{13}C$ and 0.14‰ for $\delta^{15}N$.

Stable isotope deviations are expressed in delta notation (δ), defined as the part per thousand (‰) deviation from a standard material:

$$\delta = (R_{sample} / R_{standard} - 1) \times 1000 \qquad (3)$$

where R_{sample} and $R_{standard}$ are the fractions of heavy to light isotopes in the sample and standard, respectively. The international standards were the Pee Dee Belemnite (PDB) marine fossil limestone formation from South Carolina for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$.

Data analysis. Statistical analyses were performed using the GNU R statistical system. All statistical samples submitted to tests were first checked for normality and homogeneity of the variances by Shapiro-Wilk and Bartlett tests, respectively. In the case of non-departure from normality, parametric tests were used in the subsequent analyses; otherwise, non-parametric analogs were used. The significance of differences of stable isotope signatures between tissues was tested by t-tests or Wilcoxon tests for paired samples using Do the-value correction. The influence of species on $\delta^{15}N$ and $\delta^{13}C$ measurements was tested by means of analyses of variance (ANOVA) or Kruskal-Wallis tests followed, in case of significant differences, by multiple pairwise comparison t-tests or Wilcoxon tests, respectively, for independent samples using Bonferroni's P-value correction. The influence of age and sex was tested by means of t-tests or Wilcoxon tests. Furthermore, the potential influence of length, reproductive status (GSI), and nutritional condition (HSI) of fish, as well as nutritional condition of birds (BCI) on isotope values were investigated for each species by means of Pearson's linear correlation coefficient.

Analysis of covariance (ANCOVA) was used to assess the effect of body length on $\delta^{15}N$ values of the 3 fish species. Residuals were checked for normality by means of Shapiro tests, and for homoscedasticity by plotting fitted values versus residuals. Differences in coefficients of variation were tested between the bird and fish groups, and between species within groups, using the t-test based approach described in Sokal & Rohlf (l995).

RESULTS

δ^{13}C and δ^{15}N values in liver and feathers of juvenile and adult birds, and in fish muscle are presented in Table 2. Results are given as mean $\pm$ standard deviation (SD) except when otherwise specified.

Isotope measurements in seabirds

The δ^{15}N values of feather samples were up to 1.3‰ depleted in ^{15}N compared to liver samples (Table 2). Only in juvenile white-tailed tropicbirds did these values not differ significantly (Table 3). The differences between values obtained from both tissues were even higher for δ^{13}C, as feathers were up to 2.5‰ enriched in ^{13}C in comparison to liver (Table 3).

The sex and the nutritional state of the bird influenced stable isotope signatures only in very few cases (data not shown), allowing a non-discriminant use of isotope results obtained from birds with different sexes or BCIs.

In both liver and feathers, δ^{13}C and δ^{15}N measurements differed significantly among species for juveniles and for adults (all Kruskal-Wallis tests were significant, Fig. 2). Irrespective of the subgroup considered (Fig. 2), Barau's petrels displayed the highest δ^{15}N values, and Audubon's shearwaters showed the lowest. The δ^{15}N differences between Barau's petrels and white-tailed tropicbirds were not significant. In juveniles and in the livers of adults, Barau's petrels were the most depleted in ^{13}C, followed by Audubon's shearwaters and white-tailed tropicbirds. In the feathers of adults, δ^{13}C values were lowest in Audubon's shearwaters (Fig. 2).

The differences in isotope deviations between juveniles and adults were also tested. Isotope signatures in the liver of young Barau's petrels were significantly lower than in adults (δ^{13}C: $P_{Wilcoxon} = 0.001$; δ^{15}N: $P_{Wilcoxon} = 0.020$). Hepatic δ^{13}C measurements were also significantly lower in juvenile Audubon's shearwaters than in adults ($P_{t\text{-test}} < 0.001$), although their hepatic δ^{15}N values were not ($P_{Wilcoxon} = 0.072$). Conversely, hepatic δ^{13}C and δ^{15}N values did not differ significantly in white-tailed tropicbirds ($P_{t\text{-test}} = 0.088$ and $P_{Wilcoxon} = 0.366$ respectively); feather δ^{15}N values also did not differ ($P_{t\text{-test}} = 0.377$). However, feathers of juveniles were significantly depleted in ^{13}C compared to adult feathers (Table 2; $P_{t\text{-test}} = 0.002$).

Isotope measurements in fish

There was no influence of sex or nutritional or reproductive states on isotope deviations in yellowfin tuna, skipjack tuna, and common dolphinfish (data not shown).

We noted significant positive correlations between $\delta^{15}N$ and the length of yellowfin tuna (r = 0.69; p < 0.001; n = 17) and common dolphinfish (r = 0.65; p < 0.001; n = 42; Fig. 3). For skipjack tuna, the range of sizes was narrow (41 to 85 cm), and the significance of the correlation results was borderline (r = 0.35; p = 0.067; n = 28; Fig. 3).

Differences in isotope signatures were found among species. Muscular $\delta^{13}C$ measurements differed significantly among all 3 fishes ($P_{Kruskal-Wallis} < 0.001$). Skipjack tuna was the most depleted in ^{13}C, followed in increasing order by yellowfin tuna and common dolphinfish (Fig. 4). Significant differences in $\delta^{15}N$ measurements were observed between common dolphinfish and both yellowfin and skipjack tunas ($P_{Wilcoxon} = 0.019$ and 0.001, respectively), but not between the 2 tuna species (Fig. 4). Common dolphinfish showed the lowest $\delta^{15}N$ values. The result of the ANCOVA model showed separate slopes and intercepts for each species ($P_{ANCOVA} < 0.001$, regression coefficients are displayed in Fig. 3). Fish body length influences muscular $\delta^{15}N$ values differently in the 3 species. The effect of body length was the strongest for common dolphinfish, while the slopes for yellowfin and skipjack tunas were close (Fig. 3). With respect to the length ranges, $\delta^{15}N$ values differed among individuals of equivalent length belonging to different species. Common dolphinfish exhibited the lowest predicted $\delta^{15}N$ values. Skipjack tuna showed greater $\delta^{15}N$ values than yellowfin tuna of the same body length, while large yellowfin tuna (length > 120 cm) exhibited the greatest predicted $\delta^{15}N$ values among the 3 fish species (Fig. 4).

Furthermore, the highest coefficient of variation for $\delta^{15}N$ values was observed in common dolphinfish. The difference was significant between common dolphinfish and skipjack tuna (p < 0.001) and between yellowfin and skipjack tunas (p < 0.030).

Comparing bird and fish isotope measurements

The isotope signatures of both taxonomic groups are presented jointly in Fig. 5. $\delta^{13}C$ and $\delta^{15}N$ values measured in the 3 birds and 3 fishes were compared by means of multiple pairwise comparison tests. In all but one case, isotope measurements were significantly different between bird and fish species ($P_{Wilcoxon} < 0.001$). $\delta^{15}N$ values were not significantly different between Audubon's shearwater and yellowfin tuna ($P_{Wilcoxon} = 0.145$). Furthermore, a higher variance in $\delta^{13}C$ signatures in birds was expressed by significantly higher coefficients of variation in birds than in fish (p = 0.020; Fig. 5).

DISCUSSION

Seabird trophic ecology

Because of the fast turnover of stable carbon and nitrogen isotopes in the liver, hepatic isotope signatures could be considered as indicators of adult foraging area and trophic level during the breeding season. Furthermore, isotope signatures of the feathers provide information about their trophic situation during the interbreeding period. For their nutrition, chicks exclusively depend on food brought back by their parents. Hence, isotope analyses of their liver and feathers provide information on their trophic level and on the geographic origin of prey delivered by their parents.

Feeding habits during the breeding period

Species trophic segregation

Particle organic matter $\delta^{13}C$ signatures vary from coastal to oceanic environments as well as latitudinally, with relatively well-defined shifts across frontal boundaries (Rau et al. 1982, Francois et al. 1993). The very slight increase in $\delta^{13}C$ with increasing trophic levels (Post 2002) enables $\delta^{13}C$ values in predators to serve as indicators of the water masses in which they feed (Cherel & Hobson 2007). However, a recent study over a broad latitudinal zone has evidenced weak $\delta^{13}C$ variations in tropical predatory fish of the western tropical Indian Ocean (Ménard et al. 2007). Overall, latitudinal patterns in $\delta^{13}C$ and $\delta^{15}N$ at the base of the food chain remain poorly documented in the tropical Indian Ocean. Because of these uncertainties on the isotopic patterns in this area, our isotope results cannot be interpreted in terms of well-defined foraging zones but will instead be used to delineate general trends. The $\delta^{13}C$ results (Fig. 2) obtained for juveniles (liver and feathers) and adults (liver) indicate that during the breeding period, the 3 birds prospect for food in different areas, hence avoiding competition. These conclusions are in agreement with observations made at sea. Barau's petrels have been sighted more then 1800 km south of Reunion Island during the breeding season (Stahl & Bartle 1991), whereas Audubon's shearwaters and white-tailed tropicbirds seem to feed within 80 km and hundreds of km from their colonies, respectively (Bailey 1967). None of these birds has been followed by satellite tracking. This technique would not only be very useful in completing our understanding of the dispersion of these birds at sea during and outside the breeding period, but would also indirectly allow us to study whether water particulate organic mater $\delta^{13}C$ signatures follow a decreasing gradient with increasing latitudes throughout the tropical zone of the western Indian Ocean as they do south of 30° S (Francois et al. 1993, Cherel & Hobson 2007). If this were asserted, it would be possible to use $\delta^{13}C$ signatures in birds to describe their geographic dispersion according to latitude.

δ^{15}N results show trophic differences between Audubon's shearwaters and the other species in both juveniles and adults. Lower δ^{15}N measurements in Audubon's shearwaters, the smallest species, indicate that they probably feed on prey of a lower trophic level than the other 2 seabirds. They are suspected to consume equal amounts of fish and cephalopods, whereas Barau's petrels and white-tailed tropicbirds appear to feed almost exclusively on cephalopods (98 and 80% respectively, authors' unpubl. data), which can have fairly high δ^{15}N signatures (Froese et al. 2005). These δ^{15}N results substantiate predictions of a previous study of these birds in which lower mercury levels in Audubon's shearwater were an argument for the lower trophic level of its prey (Kojadinovic et al. 2007). This is also coherent with what is known of the foraging behavior of white-tailed tropicbird and Barau's petrel. The former covers large distances to find isolated prey of large size (Ballance & Pitman 1999), and the latter shows scavenging behavior (Ballance & Pitman 1999, authors' unpubl. data), giving it the opportunity to feed on large prey of high trophic levels such as dead marine mammals or large fishes or squid. These assumptions should be regarded cautiously, since these seabirds feed in different areas that may potentially be characterized by different nitrogen baseline levels impeding a rigorous interpretation of the data.

Food provisioning strategies

Young and adult Barau's petrels showed differences in δ^{13}C and δ^{15}N values in liver. Chicks may differ from adults in their metabolism such that stable isotope fractionation during liver or feather synthesis is not consistent between chicks and adults. However, no growth-related difference has been found in the stable isotope ratios for various species (Minagawa & Wada 1984, Hobson & Sease 1998). The most parsimonious explanation for relative differences in the signatures of both isotopes in the liver of young and adult Barau's petrels is therefore that it reflects different stable isotope values in foods of young and adults rather than a systematic age-related difference in isotopic fractionation (Hobson 1993). Such differences indicate that fledglings and adults do not rely on the same prey. A probable explanation is that parents forage in separate areas when fishing for their fledglings and when fishing for themselves (lower δ^{13}C values in chicks) at which time they possibly feed on larger prey (higher δ^{15}N values in adults). Such dual food-provisioning strategies have been shown in other Procellariiformes (Chaurand & Weimerskirch 1994, Cherel et al. 2005, Congdon et al. 2005) and usually consist of parents making short foraging trips during which most of the food is brought back to their young and long trips for their own maintenance. The long trips are profitable for adults through a build up of energy reserves enabling them to maintain themselves during the short trips, which are profitable for

chicks through an increase in their feeding frequency (Cherel et al. 2005). The results obtained for Audubon's shearwaters, the other procellariiform species studied here, also support the hypothesis of an alternation of feeding areas when the food was destined to be eaten by the parent or by the chick; however, differences in $\delta^{15}N$ values were not observed. This first evidence of dual food-provisioning strategies in Barau's petrels and Audubon's shearwaters relies on fairly small differences in isotope values between chicks and adults (1.1‰ for $\delta^{13}C$ and 0.7‰ for $\delta^{15}N$ in Barau's petrel, and 0.6‰ for $\delta^{13}C$ in Audubon's shearwater) and should thus be substantiated by further investigations combining satellite tracking and isotope measurements of adults returning to the colony.

In contrast to what is observed for the procellariiform species, white-tailed tropicbird parents do not seem to discriminate their food from that fed to their young, since hepatic $\delta^{15}N$ and $\delta^{13}C$ values did not differ between age classes.

Feeding habits during the interbreeding period

Although very little precise information is available, the 3 seabird species are believed to spread out over larger oceanic areas during the interbreeding season (Bailey 1967, Stahl & Bartle 1991). During the breeding season on Reunion Island, juvenile and adult white-tailed tropicbirds had equivalent hepatic isotopic signatures implying similar diets. Consequently, isotopic deviations in feathers of juveniles were considered to be representative of isotope deviations in feathers of breeding adults.

Feather $\delta^{13}C$ values of both age classes were thus compared to investigate whether adults visit the same foraging zones during the breeding and interbreeding seasons. Although the difference in $\delta^{13}C$ values was small (0.4‰), its statistical significance, added to the weak $\delta^{13}C$ latitudinal variations in this part of the Indian Ocean (Ménard et al. 2007), suggests a shift in white-tailed tropicbird foraging areas between seasons. The extent and direction of this interseasonal shift remains unknown.

Feather $\delta^{15}N$ values of both age classes were compared to investigate whether adults maintain the same diet during the breeding and interbreeding seasons. $\delta^{15}N$ values did not differ significantly between feathers of juvenile and adult tropicbirds, indicating that the trophic levels of the latter do not change between seasons, implying that they probably maintain the same diet year-round. Moreover, when considering all 3 seabirds, we noted that the trophic distinction between

Audubon's shearwaters and the other 2 species described for the breeding season is conserved during the interbreeding season. This is another element indicating the absence of large shifts in feeding behaviors of these 3 seabirds from one season to another, although it should be kept in mind that baseline $\delta^{15}N$ values may vary between areas (Popp et al. 2007), thus affecting the above interpretations if the seabirds feed in very distinct environments.

Fish trophic ecology

Similarly to seabirds, tunas and common dolphinfish are primarily visual predators and opportunistic feeders (Roger 1994, Massuti et al. 1998, Ménard et al. 2006). They are mainly piscivorous, although they also feed on cephalopods and crustaceans (Roger 1994, Massuti et al. 1998, Potier et al. 2004). Most fish prey belong to the epipelagic fauna (small Carangidae, juvenile Scombridae) and reef fishes (Holocentridae, Tetraodontidae, Stromateidae, Mullidae; Potier et al. 2004). Differences in $\delta^{15}N$ measurements between common dolphinfish and both yellowfin and skipjack tunas (Fig. 4) suggest that the composition of common dolphinfish diet varies significantly from that of the tunas in terms of prey species and/or proportions. Yellowfin and skipjack tunas seem to occupy significantly higher trophic positions than common dolphinfish, with yellowfin tuna exhibiting the highest $\delta^{15}N$ values. This is not surprising, as yellowfin tuna tend to consume progressively larger prey as they grow (Ménard et al. 2006). For instance, large yellowfin tuna feed on other Scombridae, including skipjack tuna (Ménard et al. 2000a). The difference in diet between the dolphinfish and the tunas may also be attributable to differences in foraging behaviors (in terms of e.g. depth, feeding hours) giving common dolphinfish access to prey that differ from those available to yellowfin and skipjack tunas (Moteki et al. 2001). Adult yellowfin tuna usually feed during daylight hours in the surface mixed layer above the thermocline, although they can dive to at least 1160 m (Roger 1994, Dagorn et al. 2006. Skipjack tuna are also predominantly diurnal feeders (Roger 1994). They are limited to surface temperatures of about 17 to 30°C (Wild & Hampton 1994) and inhabit mostly the mixed layer, although they can make repetitive dives below the thermocline to depths greater than 300 m (Shaeffer & Fuller 2007). Both species also feed on nyctemeral migrating communities. Given their feeding behavior, these 2 species have access to the same prey and therefore exhibited close $\delta^{15}N$ values. Common dolphinfish are generally present from the surface up to 30 m in depth, and although they dive down to 75 m when moving in non-aggregated schools, they spend 95% of the time within 5 m from the surface (Massuti et al. 1998, Taquet 2004). Although common

dolphinfish are primarily visual predators, they can also feed at nighttime (Shcherbachev 1973). Furthermore, common dolphinfish are more associated with the FADs anchored around Reunion Island than the tunas and reside under these floating objects for much longer periods of time (Taquet 2004). Consequently, common dolphinfish potentially rely in large part on reef fishes drawn offshore that take shelter under these FADs (Bertrand et al. 2002). This idea is also supported by the significantly higher δ^{13}C values measured in this species, since coastal fauna that use benthic carbon sources, such as reef fish, are enriched in ^{13}C compared to fauna dependent on oceanic sources (France 1995).

The non-selective feeding behavior of the 3 fishes is confirmed by relatively high intraspecific coefficients of variation for δ^{15}N values that reflect a large range of prey species and/or prey sizes in their diet. The diet of tunas feeding under FADs is usually more diversified compared to the diet of unassociated individuals (Ménard et al. 2000b). In the present case, the highest coefficients of variation were observed in common dolphinfish, which suggests that their diet is relatively more varied than that of the other 2 species. This observation agrees with the idea that common dolphinfish are more closely linked to floating objects than the tunas. Part of the δ^{15}N variability might also originate from ontogenetic shifts in diet, since individuals of different sizes (and thus most probably different ages) were sampled within the same species. Larger fish are able to eat larger prey that are likely to be situated at a higher position in the food web and thus exhibit higher δ^{15}N values (Kelly 2000, Scharf et al. 2000, Ménard et al. 2007).

Trophic interactions between birds and fishes

Reunion Island is located in the South Indian tropical gyre and is considered an oligotrophic environment characterized by low productivity, which is associated with low abundance in prey, mostly distributed in patches (Ballance & Pitman 1999). Prey patches are usually associated with frontal boundaries or particular topographic features. However, these physical characteristics have little influence on tropical seabird foraging distributions, which seem to be more tightly linked to the presence of subsurface predators such as pelagic fishes (Weimerskirch et al. 2004). Subsurface predators drive prey to the surface because the air-water interface acts as a boundary that prey cannot escape. Under these circumstances, seabirds can access these same prey from the air. Presumably as a result of this pressure from below, some prey species (exocoetid flying fish and flying squids, mostly ommastrephids) have evolved a flight escape response (Ballance & Pitman 1999). While this has made them less vulnerable to predation from below, it has made

them more vulnerable to predation from above. Flying fish and squid comprise a substantial portion of the diet of many seabirds including the species studied here. A majority of Audubon's shearwater feeding events around Reunion Island occur in association with subsurface predators, and flocks are largest when they feed in association with skipjack and yellowfin tunas (Jaquemet et al. 2004). Barau's petrels are also commonly observed feeding in association with subsurface predators. Among the studied animals, white-tailed tropicbirds are the only solitary feeders that seldom associate with other birds or subsurface predators (Ballance & Pitman 1999).

In our study, Audubon's shearwaters and yellowfin tuna were characterized by similar nitrogen isotopic signatures, indicating that they feed on prey of similar trophic levels. There is probably an overlap in their diet, given that these species form the most frequently observed feeding associations in the vicinity of Reunion Island (Jaquemet et al. 2004) and that Audubon's shearwaters, contrary to the other 2 seabirds that mainly have access to flying fish and squid, dive and feed on prey under water. The other nitrogen results show that the birds generally feed at higher trophic levels than the fishes (mean δ^{15}N up to 4.1‰ higher in birds, which corresponds to about 1 trophic level; Table 2). These results are difficult to compare to other ecosystems because of the scarcity of joint isotopic studies on seabirds and pelagic fish. However, when considering separate studies on marine birds and fish conducted in the same area during the same year, it appears as though our results illustrate a situation that occurs in other parts of the world. For example in the Mediterranean Sea, δ^{15}N values for Cory's shearwater *Calonectris diomedea diomedea* and Auduin's gull *Larus andouinii* feathers were higher than those measured in the muscle of bluefin tuna *Thunnus thynnus* by 0.84 to 3.4‰ (Gómez-Díaz & González-Solís 2007, Sanpera et al. 2007, Sarà & Sarà 2007). Another example can be found in the northwestern Atlantic Sea off the Massachusetts coast, where seabird δ^{15}N values were higher than those measured in tunas: δ^{15}N values were higher by 2.3, 4.3, and 5.3‰ in common tern *Sterna hirundo* feathers than in the muscle of bluefin, yellowfin, and albacore *Thunnus alalunga* tunas respectively (Nisbet et al. 2002, Estrada et al. 2005). Consequently, although most of these 2 types of predators associate to feed, their diets do not seem to be identical. Previous studies have indeed shown that these seabirds tend to rely primarily on squid, whereas these fishes are dominantly piscivorous (Roger 1994, Moteki et al. 2001, authors' unpubl. data). The differences in nitrogen signatures might be amplified with respect to the true differences in diets due to shifts in isotopic fractionation and/or turnover rates, which might occur between tissues or taxonomic groups (DeNiro & Epstein 1978, 1981). For example, the nitrogen diet-tissue fractionation factor

determined in ring-billed gulls *L.delawarensis* is higher for liver (+2.7‰) than for muscle (+1.4‰; Hobson & Clark 1992ab), which in turn is different from that observed for Atlantic salmon *Salmo salar* muscle (+2.3‰; Persson et al. 2007).

Although no significant difference has been reported in carbon diet-tissue fractionation factors between liver and muscle in birds, a bias linked to differences in fractionation factors or turnover rates between taxonomic groups might also have affected the carbon results that show differences in foraging areas between birds and fish. The largest differences were noted between common dolphinfish and the seabirds. This result may seem surprising at first, as this fish is more epipelagic than the other 2 and could be expected to have closer isotopic signatures to the birds than the tunas. Once again, this observation may be explained by the particular foraging behaviors of common dolphinfish in relation to floating objects, which tend to increase its $\delta^{13}C$ signatures. More generally, a wider $\delta^{13}C$ range in birds (4.1‰ in birds versus 3.3‰ in fish) and higher variances in $\delta^{13}C$ values of birds indicate greater spatial distinctions in foraging areas among birds than among fish. Seabirds are flying homeothermic animals capable of covering very large distances and are much less restricted by temperatures than tunas and common dolphinfish. Their thermal regulation capacity enables them to spread to latitudes where temperatures preclude the presence of the fish species considered here. For example, Barau's petrels have been sighted more then 1800 km south of Reunion (Bailey 1967, Stahl & Bartle 1991), which roughly corresponds to 38° S, whereas skipjack tuna, which of the 3 fishes are adapted to the lowest temperatures, are limited by the 17°C isotherm situated around 30° S in the western part of the Indian Ocean. According to the known feeding behaviors of these animals and the above isotope results, we suggest that these 2 taxonomic groups forage somewhat in different water masses but feed in association to reduce foraging effort when present in the same areas.

CONCLUSION

This study is the first to focus on the trophic ecology of an assemblage of marine pelagic fishes and seabirds from Reunion Island, including the endemic Barau's petrel. Our results revealed that during the breeding period, Barau's petrels, Audubon's shearwaters, and white-tailed tropicbirds show differences in the ecological niches they occupy and suggest that both Procellariiformes might adopt a dual food-provisioning strategy, making separate foraging trips to feed their fledglings and for their own maintenance. Furthermore, evidence suggests that white-tailed

tropicbirds change foraging areas between breeding and molting seasons, although no diet shift seems to occur.

Our results also support the idea that differences in feeding strategies exist among the 3 fishes close to Reunion Island. Common dolphinfish presumably prey more on low trophic level coastal organisms than yellowfin and skipjack tunas, which are more associated with birds, namely Audubon's shearwaters, during feeding events. These results on species associations confirm prior reports of at-sea observations. Additionally, our study corroborates the previously established strong aggregative behavior of common dolphinfish to FADs floating or anchored around Reunion Island.

To further investigate the diet and spatial distribution of these top predators, isotopic baselines of $\delta^{13}C$ and $\delta^{15}N$ in marine pelagic food webs, stable isotope values in potential prey, and satellite tracking data are needed.

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Figure captions

Fig. 1. Reunion Island in the western Indian Ocean

Fig. 2. Variation in isotopic deviations among bird species from Reunion Island and the studied tissues separately (mean ±SE). (A,B) Adults, (C,D) juveniles; (A,C) liver, (B,D) feathers. PB: Barau's petrel; PLB: Audubon's shearwater; PL: white-tailed tropicbird. Full species names in Table 2. Significance of the differences in δ^{13}C and δ^{15}N values among species indicated along the *x*- and *y*-axes, using Latin and Greek letters, respectively

Fig. 3. Pelagic fishes from Reunion Island. Linear regression of δ^{15}N measurements against fish lengths in yellowfin tuna (YFT), skipjack tuna (SKJ), and common dolphinfish (COR). Full species names in Table 2. Parameters are those obtained by ANCOVA

Fig. 4. Pelagic fishes from Reunion Island. Variation in isotopic deviations among fishes (mean ±SE). YFT: yellowfin tuna; SKJ: skipjack tuna; COR: common dolphinfish. Full species names in Table 2. Significances of the differences in δ^{13}C and δ^{15}N values among species indicated along the *x*- and *y*-axes, using Latin and Greek letters, respectively

Fig. 5. Trophic segregation of seabirds and marine fishes from Reunion Island based on δ^{13}C and δ^{15}N measurements in bird liver (juveniles and adults combined) and fish muscle (mean ±SE). PB: Barau's petrel; PLB: Audubon's shearwater; PL: white-tailed tropicbird; YFT: yellowfin tuna; SKJ: skipjack tuna; COR: common dolphinfish. Full species names in Table 2

Table 1. *Thannus albcares*, *Katsuwonus pelamis* and *Coryphaena hippurus*. Relationships between weight and length for 3 tropical pelagic fishes: data from
studies in the Indian Ocean. These relationships are presented as exponential regressions
on the following model: $W = a$
$\times L^b$ where W is the weight and L the length

Species	n	a	b	r²	Source
Yellowfin tuna (females)	194	54.10^{-6}	2.72	0.97	Tantivala (2000)
Yellowfin tuna (males)	174	41.10^{-6}	2.79	0.97	Tantivala (2000)
Skipjack tuna	22	$6.65.10^{-6}$	3.28	0.98	Present study
Common dolphinfish	51	$5.94.10^{-6}$	3.04	0.93	Present study, Bourjea pers. comm.

Table 2. ^{13}C and ^{15}N values ( ) of seabirds and pelagic fishes from Reunion Island. CV: coefficient of variation.
Shaded areas correspond to data representing the trophic behavior of adult birds at sea

during the inter-

breeding season

White-tailed tropicbird	Juvenile	Liver	17	**-17.9 ± 0.8**	**14.2 ± 2.2**
				4.5 (-19.7 / -17.5)	15.3 (11.4 / 20.4)
		Feathers	17	**-15.6 ± 0.45**	**13.4 ± 1.1**
				2.9 (-16.3 / -14.9)	8.5 (11.6 / 15.0)
	Adult	Liver	32	**-17.5 ± 0.6**	**14.4 ± 1.4**
				3.5 (-19.4 / -16.2)	9.8 (12.1 / 18.1)
		Feathers	31	**-15.2 ± 0.3**	**13.7 ± 1.0**
				2.0 (-15.7 / -14.5)	7.5 (10.7 / 15.5)
Fish					
Yellowfin tuna	107 ± 34	Muscle	20	**-16.3 ± 0.3**	**12.0 ± 1.0**
	63 / 170			1.9 (-16.7 / -15.5)	8.5 (10.0 / 13.8)
Skipjack tuna	68 ± 15	Muscle	37	**-16.8 ± 0.3**	**11.9 ± 0.6**
	41 / 85			2.1 (-17.8 / -16.0)	5.2 (10.7 / 13.2)
Common dolphinfish	87 ±15	Muscle	45	**-15.8 ± 0.6**	**11.1 ± 1.1**
	61 / 112			3.8 (-17.3 / -14.5)	9.7 (9.5 / 13.7)

Table 3. Comparison of stable isotopic signatures in liver and feathers of seabirds and pelagic fishes from Reunion Island. Full species names in Table 2. Significant results are in **bold**

	n	$\delta^{13}C$	$\delta^{15}N$
Juveniles			
Barau's petrel	25	$\mathbf{P_{\textit{t}\text{-test}} < 0.001}$	$\mathbf{P_{\textit{t}\text{-test}} = 0.005}$
Audubon's shearwater	37	$\mathbf{P_{\textit{t}\text{-test}} < 0.001}$	$\mathbf{P_{\textit{t}\text{-test}} < 0.001}$
White-tailed tropicbird	17	$\mathbf{P_{\textit{t}\text{-test}} < 0.001}$	$P_{\text{Wilcoxon}} = 0.517$
Adults			
Barau's petrel	14	$\mathbf{P_{\textit{t}\text{-test}} < 0.001}$	$\mathbf{P_{\textit{t}\text{-test}} = 0.007}$
Audubon's shearwater	21	$\mathbf{P_{\textit{t}\text{-test}} < 0.001}$	$\mathbf{P_{\textit{t}\text{-test}} = 0.007}$
White-tailed tropicbird	31	$\mathbf{P_{\textit{t}\text{-test}} < 0.002}$	$\mathbf{P_{\textit{t}\text{-test}} = 0.009}$