Stable Isotopes Confirm Community Patterns in Foraging Among Hawaiian Procellariiformes

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Abstract.—Stable-isotope analysis of whole blood was used to examine the feeding of adults and chicks of five seabirds (Wedge-tailed *Puffinus pacificus* and Christmas Shearwaters *P. nativitatus*, Bonin *Pterodroma hypoleuca* and Bulwer's Petrels *Bulweria bulwerii* and Tristram's Storm-petrel *Oceanodroma tristrami)* in the northwestern Hawaiian Islands. The goal was to compare community foraging patterns as determined by stable-isotope analysis with traditional studies conducted in the early 1980s. Furthermore, chick-rearing Procellariiformes have been hypothesized to practice a bimodal food-provisioning strategy, a behavior yet to be documented in any of the northwestern Hawaiian Islands species outside the albatrosses. Except for Christmas Shearwaters, adults and chicks had significantly different isotope ratios, suggesting differential self- and chick-provisioning by adults. Wedge-tailed Shearwaters foraged opportunistically for themselves, while providing prey of higher trophic position to their chicks. Bulwer's Petrel and Tristram's Storm-petrel adults likely brought prey of more uniform trophic position to their chicks, while relying on more permanent prey patches differing in composition for themselves during the breeding season. Results suggested little overlap in stable-isotope ratios among species and were likely a result of behavioral and morphological differences in feeding. *Received 12 February 2009, accepted 1 October 2009.*

Key words.—foraging, French Frigate Shoals, Hawaiian Islands, Procellariiformes, stable isotopes.

The feeding ecology and diets in tropical and subtropical seabird communities are represented in the literature from only a handful of comparative studies, most dating back 25 years or more (e.g. Ashmole and Ashmole 1967; Diamond 1983; Harrison *et al.* 1983), and some more recent studies (e.g. Spear *et al.* 2007; Cherel *et al.* 2008; Jaquemet *et al.* 2008; Catry *et al.* 2009). The diets of several species were described from a small number of well-digested prey items (Harrison *et al.* 1983) and because they relied on regurgitations or stomach contents, could be biased against soft-bodied organisms like invertebrates, which remain in the gut for a much greater time as compared with the hard parts of a squid or fish (Duffy and Jackson 1986; Barrett *et al.* 2007). Such samples may not necessarily represent adult diet if they were collected from chicks or provisioning adults

(e.g. Hodum and Hobson 2000; Forero *et al.* 2005; Hedd and Montevecchi 2006).

The use of stable isotopes of carbon and nitrogen to investigate seabird foraging and trophic niche width is well established in the literature (e.g. Hobson *et al.* 1994; Thompson *et al.* 1999; Bearhop *et al.* 2004; Forero *et al.* 2004). By assuming that prey species differ in isotopic composition, that there is minimal change in basal isotope ratios over a short time frame, and that the tissue of interest reflects the period of dietary integration in question, stable isotopes can provide a measure of trophic niche width on a single scale, making it comparable both within and across communities. Sub-tropical seabirds, a group whose diet is generally less known than their temperate or polar counterparts (Harrison *et al.* 1983; Ballance and Pitman 1999), have recently been the focus of several studies incor-

porating stable-isotope analysis (SIA) (e.g. Cherel *et al.* 2008; Jaquemet *et al.* 2008; Kojadinovic *et al.* 2008; Catry *et al.* 2009).

The concept of interspecific resource partitioning during the breeding season has received much attention in early seabird community studies (e.g. Ashmole and Ashmole 1967; Pearson 1968; Diamond 1983), and studies incorporating stable isotopes of carbon and nitrogen to investigate resource partitioning have increased in recent years (e.g. Awkerman *et al.* 2007; Cherel *et al.* 2008). To our knowledge, there have been no similar studies of tropical or subtropical Procellariiformes in the Pacific Ocean outside the albatrosses.

Advancements in satellite telemetry, geolocators and SIA have led to increased documentation of a bimodal foraging strategy in numerous seabird species in which adults do not rely on the same resources in which they feed their chicks (Chaurand and Weimerskirch 1994; Catard *et al.* 2000; Cherel *et al.* 2008) Such trophic segregation is thought to derive from adults alternating between short, energetically costly foraging trips to feed chicks, and long foraging trips in which adults restore their body reserves (Weimerskirch *et al.* 2003). The strategy has been documented in several Procellariiformes (Chaurand and Weimerskirch 1994; Congdon *et al.* 2005; Kojadinovic et al. 2008) but has yet to be observed in any of the northwestern Hawaiian Islands species outside the albatrosses.

Overall, our goal was to examine differences in adult self- and chick-provisioning among five sub-tropical Procellariiform seabirds—Bonin Petrel *Pterodroma hypoleuca*, Bulwer's Petrel *Bulweria bulwerii*, Christmas Shearwater *Puffinus nativitatus*, Tristram's Storm-petrel *Oceanodroma tristrami* and Wedge-tailed Shearwater *P. pacificus* and to investigate differences in niche width and overlap as indicated by stable-isotope ratios of carbon and nitrogen.

METHODS

We collected whole blood from both adults and chicks of the five aforementioned Procellariiform sea-

birds. We also sampled feathers from Tristram's Storm-petrel, the least-known of the species in terms of foraging ecology. Blood isotope ratios show an integration of diet from the previous two weeks and feathers integrate diet from the period at which they were grown (Hobson and Clark 1992), therefore removing much of the variation caused by eruptive or "burst" feeding by consumers (Huettmann *et al.* 2005). A summary of foraging behavior and predominant prey items for each species is presented in Table 1.

Sample Collection and Preparation

Blood samples were collected on Tern Island, French Frigate Shoals, Hawaiian Islands (23°52.13'N, 166°17.16'W) during the breeding seasons of 2005-2006. Chicks were sampled as close to fledging as possible, at the same time as unrelated adults, and the timing depended on each species' breeding phenology. Birds were captured by hand on the surface and approximately 1-2 μl of whole blood was taken from the brachial vein. Blood was either stored in 70% ethanol or freeze-dried. Neither preservation method has a significant effect on stable-isotope ratios (Hobson *et al.* 1997, but see Bugoni *et al.* 2008).

Between four and six worn breast feathers from adult Tristram's Storm-petrels were opportunistically collected during the winter 2005-2006 breeding season. We did not collect blood samples from these individuals. For Tristram's Storm-petrel, body molt is not known (P. Pyle, pers. comm.), but based on other hydrobatids, it likely occurs in the months immediately prior to breeding (Ainley *et al.* 1976; Monteiro *et al.* 1996; Pyle 2008), which for Tristram's Storm-petrel would be September-November (McClelland et al. 2008).

Prey samples (equivalent to chick meals) were collected from regurgitating birds in 2005; only those identifiable and in good condition were kept for analysis. All prey samples were <100 mm and therefore fit the feeding range of all our focal species. Amphipod, water strider (*Halobates* sp.) and euphausiid samples were kept in 25% formalin, which does alter $\delta^{13}C$ values slightly, but values were corrected prior to analysis by 1.65‰ (Sarakinos *et al.* 2002). In addition, collected samples included muscle and eggs from flying fish (Exocoetidae) and squid. Other possible prey items (Table 1) were not collected, as they were not identified in regurgitated samples.

Stable-isotope Analysis

Prey items were corrected mathematically for lipid content (Post *et al.* 2007), yielding changes in $\delta^{13}C$ of 0.07-2.33‰, depending on the tissue's lipid content, as determined by C:N. For the comparison of Tristram's Storm-petrel diet, we applied relative discrimination factors to compensate for comparing different tissues (Cherel *et al.* 2005). Past studies have found $\delta^{15}N$ blood discrimination factors to be 60 ± 1.2% of feather discrimination factors (Bearhop *et al.* 2002; Cherel *et al.* 2005), so we used the mean factors of 2.5‰ and 4.2‰ for blood and feathers respectively to compare feather and whole blood stable-isotope ratios. Furthermore, recent evidence suggests that differences in stable-isotope ratios between blood and feathers are consistent across species and age classes (Quillfeldt *et al.* 2008).

Stable-isotope analysis was conducted at the Queen's Facility for Isotope Research in Kingston, Ontario, Can-

Table 1. Summary of the known feeding ecology and behavior in five Procellariiform seabirds.

Species	Foraging Habitat	Breeding Season	Prey Capture	Main Prey Items	References
Bonin Petrel	Offshore, surface, nocturnal	Winter	Surface-seizing/dipping	Unidentified fish & squid, Myctophidae (lanternfish), Sternoptychidae (hatchetfish), Unidentified crustaceans	(Harrison et al. 1983; Seto and O'Daniel 1999)
Bulwer's Petrel	Offshore, surface, nocturnal	Summer	Surface-seizing/dipping	Unidentified fish & squid, Myctophidae, Sternoptychidae, Water striders (Halobates)	(Harrison et al. 1983; Megyesi and O'Daniel 1997; Mougin and Mougin 2000)
Christmas Shearwater	Offshore, surface, diurnal	Summer	Surface-seizing, shallow pursuit-plunging	Ommastrephid squid, Mullidae (goatfish), Exocoetidae (flying fish)	(Ashmole and Ashmole 1967; Harrison et al. 1983; Seto 2001)
Wedge-tailed Shearwater	Offshore surface diurnal & nocturnal	Summer	Surface-seizing/dipping	Mullidae, Carangidae (jacks and scads), Ommastrephid squid	(King 1974; Harrison et al. 1983; Whittow 1997)
Tristram's Storm-petrel	Offshore, surface, nocturnal	Winter	Surface-dipping	Unidentified squid, Velellidae (Hydrozoa), Unidentified fish, Water striders (Halobates)	(Harrison et al. 1983; Slotterback 2002)

ada. Before analysis, feathers were washed in 2:1 chloroform:methanol solution for 24h, rinsed in distilled water, and left to air-dry for 48h. Samples of 0.10-.15 mg of freeze-dried blood and feathers cut with stainless steel scissors were weighed into tin capsules and combusted in a TC Elemental Analyser with the resultant gasses passed through a Finnigan MAT Delta Plus XL isotope mass spectrometer. Concurrent international and in-house standards (reported as mean ± SE) for carbon (NBS 21 graphite: -28.0‰ ± 0.1, n = 35; and UC-1 graphite: -5.8‰ ± 0.2, n = 28) and nitrogen (RM 8548 ammonium sulphate: 19.9‰ ± 0.4, n = 43) were used to measure instrument accuracy. Samples had high repeatability within runs, as determined by duplicates samples in each run, producing mean differences of 0.2‰ for carbon and 0.2‰ for nitrogen across all tissue types.

Statistical Analysis

All analyses were conducted in SPSS 16 (SPSS Inc., 2007). We used multivariate analysis of variance (MANOVA) to assess differences among species and age classes in stable-isotope ratios, with univariate analysis of variance (ANOVA) to examine each isotope ratio separately in cases where the MANOVA revealed a significant difference. *Post-hoc* multiple comparisons were done using the Ryan's Q test (Ryan 1959; Day and Quinn 1989) or Games-Howell test (Games and Howell 1976) and homogeneity of variance was assessed using Levene's test. Because Ryan's Q test reports the probability that a group is not similar (so that identical groups have p = 0.00 and completely dissimilar groups have p = 1.00, Ryan 1959, 1960), we report p-values as $1-p_Q$ where p_Q is the result from Ryan's Q test. All tests were considered significant with p ≤ 0.05.

We did not compare prey and consumer species directly because of other unknown confounding factors affecting isotope ratio differences between prey and consumers (Inger and Bearhop 2008). The use of chicks that had reached fledging age reduces effects of growth on stable-isotope ratios (Sears *et al.* 2009) and so we felt that adult-chick comparisons were valid (Cherel 2008).

RESULTS

Differences Among Species

Adult seabirds. Both isotope ratios had homogenous variances within groups (Levene's test, all p > 0.09) and there were significant differences among species in both isotope ratios (MANOVA, Wilks' λ = 0.066, $F_{8,86}$ = 31.01, p < 0.001), so isotopes were examined individually. There were significant differences in both δ13C (ANOVA, $F_{4,44}$ = 35.41, p < 0.001) and δ15N (ANOVA, $F_{4,44}$ = 29.74, p < 0.001). Bonin Petrels and Wedge-tailed Shearwaters had similar δ13C values (Ryan's Q, p = 0.99), as did Christmas Shearwaters and Tristram's Storm-petrels (Ryan's Q, p =

0.94). Bulwer's Petrels were intermediate, but significantly different from the other two groups (Ryan's Q, p < 0.001; Fig. 1). Wedge-tailed Shearwaters occupied the lowest trophic position as indicated by $\delta^{15}N$ (Ryan's Q, p < 0.001), followed by Tristram's Storm-petrel and Bonin Petrels (Ryan's Q, p = 0.86), although Bonin Petrels were not significantly different from Christmas Shearwaters and Bulwer's Petrels in $\delta^{15}N$ (Ryan's Q, p = 0.60; Fig. 1).

Seabird chicks. Stable-isotope ratios in chicks also had homogenous variances (Levene's test, all p > 0.32), and again there were significant differences among species (MANOVA, Wilks' λ = 0.042, $F_{6,74}$ = 47.746, p < 0.001). Both $\delta^{13}C$ and $\delta^{15}N$ were different among species (ANOVA, $F_{3,48}$ = 5.65, p = 0.003, $F_{3,48}$ = 188.20, p < 0.001 respectively). Multiple comparisons revealed two groups based on $\delta^{13}C$—Tristram's Storm-petrel and Wedge-tailed Shearwaters (Ryan's Q, p < 0.001) were more depleted in ^{13}C than Christmas Shearwaters and Bulwer's Petrels (Ryan's Q, p = 0.045). All four species had significantly different trophic positions (Ryan's Q, all p < 0.001), and in increasing order of $\delta^{15}N$ were Tristram's Storm-petrel < Bulw-

er's Petrel < Christmas Shearwater < Wedge-tailed Shearwater (Fig. 1).

Differences Between Age Classes

Comparisons between age classes (adult and chick) were possible in four species. Bulwer's Petrel adults had lower $\delta^{13}C$ (ANOVA, $F_{1,18}$ = 4.96, p = 0.04) and higher $\delta^{15}N$ (ANOVA, $F_{1,18}$ = 11.35, p < 0.001) than chicks. Tristram's Storm-petrels followed the same pattern for $\delta^{15}N$ (ANOVA, $F_{1,21}$ = 46.24, p < 0.001), but chicks had a lower $\delta^{13}C$ (ANOVA, $F_{1,21}$ = 34.10, p < 0.001). Wedge-tailed Shearwater adults fed at a lower trophic position (ANOVA, $F_{1,18}$ = 86.68, p < 0.001) and had lower $\delta^{13}C$ (ANOVA, $F_{1,18}$ = 6.11, p = 0.02) than chicks, while Christmas Shearwater adults and chicks did not differ in either $\delta^{13}C$ (ANOVA, $F_{1,22}$ = 0.232, p = 0.64) or $\delta^{15}N$ (ANOVA, $F_{1,22}$ = 0.752, p = 0.40).

Tristram's Storm-petrel

There were significant differences in the isotope ratios between tissues (MANOVA, Wilks' λ = 0.52, $F_{2,27}$ = 7.75, p = 0.004), so ratios were analyzed separately. While there were differences in $\delta^{13}C$ between tissues (ANOVA, $F_{1,18}$ = 15.99, p = 0.001), with blood more enriched in ^{13}C, there were no differences in $\delta^{15}N$ between tissues (ANOVA, $F_{1,18}$ = 2.02, p = 0.17).

Niche Width

Variances in whole blood isotope ratios are presented in Table 2. Among adults, Bonin Petrels showed the lowest variance in both isotope values, and among chicks, Bulwer's Petrels had the lowest $\delta^{15}N$ variance and Wedge-tailed Shearwaters the lowest $\delta^{13}C$ variance. In all cases, chick $\delta^{13}C$ variance was greater than the adults', but for all but Christmas Shearwater, adult $\delta^{15}N$ variance was greater. The greatest variance was seen in Wedge-tailed Shearwater adults' $\delta^{15}N$ value.

Prey Species

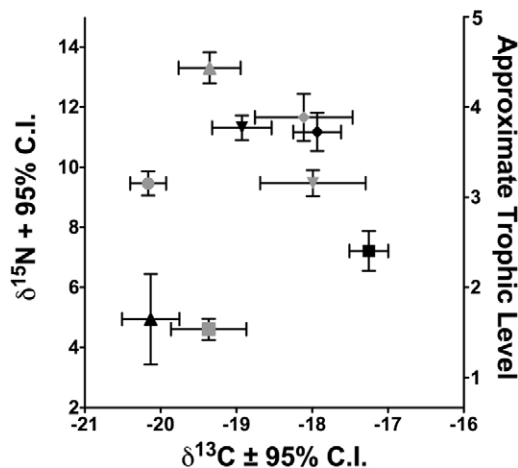Prey species did not have homogeneous variances (both $\delta^{13}C$ and $\delta^{15}N$, Levene's test

Figure 1. Trophic relationships of adults and chicks of Bonin Petrels (circle), Bulwer's Petrels (inverted triangles), Christmas Shearwaters (diamonds), Tristram's Stormpetrels (squares) and Wedge-tailed Shearwaters (triangles) in the Northwest Hawaiian Islands. Adults (black symbols) and chicks (grey symbols) of the same species have the same symbol shape. Sample sizes are given in Table 2.

Table 2. Variances of whole blood isotope ratios in Procellariiform seabirds as a measure of niche width.

| Species	Age Class	n	Variance δ^{13}C	Variance δ^{15}N
Bonin Petrel	Adult	4	0.10	0.28
Bulwer's Petrel	Adult	12	0.57	2.03
Bulwer's Petrel	Chick	8	1.30	0.50
Christmas Shearwater	Adult	14	0.42	1.67
Christmas Shearwater	Chick	10	1.32	1.93
Tristram's Storm-petrel	Adult	9	0.89	3.31
Tristram's Storm-petrel	Chick	14	1.04	0.52
Wedge-tailed Shearwater	Adult	10	0.46	7.22
Wedge-tailed Shearwater	Chick	10	0.53	0.85

< 0.04). There were significant differences among prey species in isotope ratios (MANOVA, Wilks' λ = 0.11, $F_{10,60}$ = 12.31, p < 0.001) so each ratio was examined individually. Significant differences were present for both carbon (ANOVA, $F_{5,31}$ = 24.82, p < 0.001) and nitrogen isotope ratios (ANOVA, $F_{5,31}$ = 5.96, p = 0.001; Fig. 2). Games-Howell post-hoc tests (GH test) found two groups based on δ^{13}C: amphipods (GH, all p < 0.002) and all other prey species (GH, all p > 0.10). By trophic position, flying fish muscle and eggs were similar to all other prey species (GH, all p > 0.19), with squid lower than euphausiids (GH, p = 0.0015), which were

lower than amphipods (GH, p = 0.045). Water striders had a similar trophic position to both squid and euphausiids (GH, all p > 0.51).

DISCUSSION

All species share many of the same common prey types (Table 1), yet we found that there was no overlap in adult isotope signatures among species, suggesting segregation either in prey composition, prey size, space or time. The range of δ^{13}C values are consistent with offshore foraging seabirds (France 1995), with adult Tristram's Storm-petrels the most enriched and adult Bonin Petrels and Wedge-tailed Shearwaters the most depleted in ^{13}C. The difference between these groups is ~3‰, and all species considered here are classified as offshore feeders (Diamond 1983; Fefer et al. 1984). However, the range of δ^{15}N values span several trophic levels and cover approximately 9‰, or 2-3 trophic levels (Minagawa and Wada 1984). Adult seabirds fell into one of two broad groups—Wedge-tailed Shearwaters and Tristram's Storm-petrels with lower trophic positions (δ^{15}N < 8‰), and all other species with higher positions (δ^{15}N > 9‰).

Disparity both in trophic position and in the variance in δ^{13}C observed between adults and chicks in three species (Wedge-tailed Shearwater, Bulwer's Petrel and Tristram's Storm-petrel) suggests that adults employed a bimodal foraging strategy. The behavior has previously been documented in Laysan (*Phoebastria immutabilis*) and Black-footed (*P.*
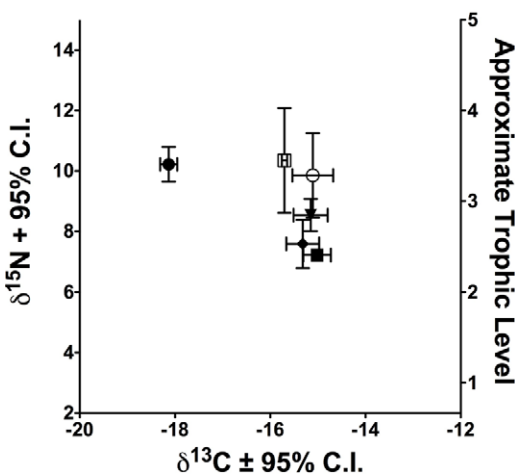
Figure 2. Trophic relationships among common seabird prey groups from the northwest Hawaiian Islands; Amphipods (black circle), Euphausiids (black inverted triangle), Flying Fish Eggs (white square), Flying Fish Muscle (white circle), Squid (black square) and Water Striders (black diamond). Sample sizes are given in Table 2.

nigripes) Albatrosses breeding in the north-western Hawaiian Islands (Hyrenbach *et al.* 2002). To our knowledge this is the first evidence of the behavior in the smaller Procellariiforms breeding in the island chain.

The bimodal foraging strategy in Wedge-tailed Shearwaters suggested by this study is in direct contrast to Baduini (2002)'s study of the same colony which found shearwaters employed a unimodel foraging strategy. Our results correspond more with those of Wedge-tailed Shearwaters in Australian tropical waters (Congdon *et al.* 2005). Procellariiforms have been documented switching from a unimodal to a bimodal foraging strategy when feeding conditions are poor (Granadeiro *et al.* 1998). We suggest the disparity between the two studies is likely due to less optimal local foraging conditions during the period of this study.

Christmas Shearwater adults and chicks had a similar diet as determined by SIA, although chicks had a larger niche width in both isotope ratios. Compared to Wedge-tailed Shearwaters, Christmas Shearwaters have higher wing-loading (Hertel and Ballance 1999), and therefore forage closer to their colony. Christmas Shearwaters also pursue prey by diving (Ashmole and Ashmole 1967), whereas Wedge-tailed Shearwaters often pursue aerially (Hertel and Ballance 1999). Harrison *et al.* (1983) found fewer prey items per load as compared to Wedge-tailed Shearwaters, which suggests higher caloric value per individual item, and is supported by the higher trophic position of adults in this study. The higher $\delta^{13}C$ value also supports the idea that Christmas Shearwaters forage closer to shore than Wedge-tailed Shearwaters.

The diet of Bonin Petrels is known only from Harrison *et al.* (1983) who found 13 fish families and seven crustacean families in the 144 highly digested samples they collected. Bonin Petrel adults had the smallest niche width of any species or age class, which suggests a more specialized diet if the assumptions presented here and in Bearhop *et al.* (2004) hold true. Most Bonin Petrels are found in waters between 20-28°C (Kuroda 1991), typically cooler than either Bulwer's

Petrel or Wedge-tailed Shearwater, suggesting higher ocean productivity (Ballance and Pitman 1999), and more reliable prey distribution, and therefore allowing a more specialized diet as compared to either of the shearwaters.

Bulwer's Petrels feed extensively at night (Harrison *et al.* 1983) near the surface (Mougin and Mougin 2000), and the large number of invertebrates in their observed diet, especially water striders (Cheng and Harrison 1983; Spear *et al.* 2007) are those associated with fish, and could be unintentionally consumed (Zonfrillo 1986) or the result of "burst feeding" as with Bonin Petrels. Niche width in chicks was the smallest in $\delta^{15}N$, but only smaller in $\delta^{13}C$ than Christmas Shearwater. To our knowledge, the differences in isotopic signatures between adults and chicks documented in this study are the first to suggest a bimodal foraging strategy in this wide-ranging species.

The diet of Tristram's Storm-petrel is largely unknown with only one published study (Harrison *et al.* 1983) which suffered from small sample size (n = 10). Our results suggest that, similar to Bulwer's Petrel, adults forage for themselves in a smaller geographic area, but consume a wider variety of prey than they provide to chicks. The relatively high variance in $\delta^{15}N$ and $\delta^{13}C$ found in adults implies a highly opportunistic foraging pattern. This is consistent with the large number of water striders and the hydrozoan *Velella velella*, both considered an opportunistic prey, from previous work (Cheng and Harrison 1983; Harrison *et al.* 1983).

The differences between blood and feather $\delta^{13}C$ ratios suggest another prebreeding foraging strategy. Adults are present at the colony for one-two months prior to breeding (McClelland *et al.* 2008), and therefore may choose a wider geographic range to search for preferred prey as they are not burdened with supplying the nutritional demands of a chick (Wernham and Bryant 1998).

Because we lack the proper adjustments to perform multi-source mixing model at present (Phillips and Gregg 2003), our interpretations here are qualitative in relation to

seabird consumers. Amphipods had the lowest $\delta^{13}C$ values, but were enriched over those presented in Hedd and Montevecchi (2006), likely because of our correction for the effects of preservative. All other prey species fell in a small range (~1‰) along the $\delta^{13}C$ scale. That amphipods had the highest trophic position is puzzling. A more complete sampling of possible prey species identified in Harrison *et al.* (1983) should be undertaken to allow for a quantitative analysis similar to that produced by Hedd and Montevecchi (2006).

Although some studies have indicated that lipid removal from avian blood is unnecessary (Bearhop *et al.* 2000; Cherel *et al.* 2005), neither study included Procellariiformes, which are unique among seabirds in providing their young with regurgitated prey mixed with lipid-rich oil (Place *et al.* 1989). However, we feel that our comparisons within this order remain valid.

At the community level, we found no overlap among species in either age class, which suggests geographical, temporal or trophic segregation. Diamond (1983) suggested pelagic-feeding seabirds should have less diverse diets, and therefore more overlap than inshore feeders, such as terns and noddies (subfamily Sterninae), but we found very little evidence of overlap among species, a similar conclusion to Spear *et al.* (2007) in the eastern tropical Pacific, and to Cherel *et al.* (2008) in the Indian Ocean. A more rigorous assessment of overlap should consider other pelagic species, namely Laysan and Black-footed Albatrosses, as well as boobies (Sulidae) and tropicbirds (Phaethontidae). Forero *et al.* (2004) suggested that coexistence of predators should occur only when there is an overabundance of prey or a diversification of morphology or feeding behavior. Since tropical and subtropical oceans are typically low in productivity and do not experience seasonality as much as temperate waters (Ballance *et al.* 2006), we suggest that diversification of morphology or behavior is the reason for low overlap among these five species. Greater knowledge is required about the isoscapes, or patterns of isotope ratios, across the Pacific Ocean among sea-birds in order to make conclusions about foraging locations based on seabird stable-isotope ratios, and this is currently lacking (e.g. Cherel *et al.* 2008). This study, however, provides unique insight into the foraging ecology of these little-studied species, and suggests additional studies incorporating bird-mounted recording tags to understand the foraging behavior of north Pacific Procellariiformes.

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