COMPARATIVE FORAGING ECOLOGY IN THE DARK TERN GUILD BREEDING OFF SOUTHWESTERN AUSTRALIA — INSIGHTS FROM STABLE ISOTOPE ANALYSIS

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SUMMARY

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This paper uses stable isotope analysis to examine the foraging ecology of the tropical "dark" terns breeding in the subtropics off southwestern Australia and wintering at lower geographic latitudes. The $\delta^{13}C$ and $\delta^{15}N$ values of feathers and eggshell membranes indicated that Brown Noddies *Anous stolidus* breeding in this region were foraging in waters characterised by higher inorganic nitrogen availability and productivity than those occupied by Bridled Terns *Onychoprion anaethetus*. However, Bridled Terns probably foraged at a higher trophic level than Brown Noddies, and this was probably related to their habit of foraging on a range of marine organisms associated with floating rafts of macro-algae and other flotsam. The $\delta^{13}C$ and $\delta^{15}N$ values of adult primary feathers indicated that Sooty Terns *Onychoprion fuscata* and Bridled Terns foraged in wintering areas close to the equator, but Sooty Terns again utilised more productive water masses. The Brown Noddies breeding off southwestern Australia appear to winter closer to the subtropics than Bridled and Sooty Terns.

Key words: Bridled Tern, Brown Noddy, Sooty Tern, foraging habitat, stable isotopes $\delta^{13}C$ $\delta^{15}N$, southwestern Australia

INTRODUCTION

The dark tern guild

The Bridled Tern *Onychoprion anaethetus*, Sooty Tern *Onychoprion fuscatus*, Brown Noddy *Anous stolidus* and Lesser Noddy *Anous tenuirostris* comprise an ecological guild of generally sympatric, pelagic, contact-dipping "dark" terns occupying much of the tropical Indian Ocean (Cramp 1985). In some locations, such as at the Abrolhos Islands of southwestern Australia, this guild also inhabits subtropical waters (Surman & Wooller 2003, Dunlop 2009). Since 1900 the Bridled Tern, Sooty Tern and Brown Noddy have established new "frontier" colonies on continental islands south of the Houtman Abrolhos (Fig. 1). The population dynamics of the tropical seabird populations (including the "dark" terns) undergoing distributional change off southwestern Australia were reviewed in a previous paper (Dunlop 2009). This paper presents a perspective on the foraging ecology of the "dark tern" guild enlightened by a stable isotope analysis from breeding colonies in the subtropical waters off southwestern Australia.

The prey species taken by the dark terns breeding on islands in the region have been well documented (Gaughan *et al.* 2002, Surman & Wooller 2003, Surman & Nicholson 2009, Dunlop 1997). Post-larvae of the Beaked Salmon *Gonorhynchus greyi,* occasionally supplemented by the post-larvae of Australian Anchovy *Engraulis australis* or by squid, dominate the diet of Brown Noddy in this region (Gaughan *et al.* 2002, Surman & Wooller 2003, Surman & Nicholson 2009). Both fish post-larvae were abundant in regurgitated boluses collected from incubating Brown Noddies on 30 October 2009.

The diet of the Bridled Tern in the region is diverse and contains a variety of organisms with obligate or facultative associations with floating *Sargassum* rafts. The most frequently taken prey type is the epipelagic post-larval stage of the Black-spotted Goatfish *Parupeneus signatus* (Dunlop 1997).

Stable isotope analysis

Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) occur naturally in the environment. The ratios of the heavier isotopes to the common forms are changed by the physical sorting of biological processes such as photosynthesis in plants, or food digestion or metabolism in microbes and animals. These changes in the isotopic ratio are referred to as fractionation. The values given to the stable isotope ratios ($\delta^{13}C$ or $\delta^{15}N$) are measured in parts per thousand (‰) and may be positive or negative because they represent deviations from the values of standard materials (Kelly 2000, Bond & Jones 2010, Graham *et al.* 2010).

Both $\delta^{13}C$ and $\delta^{15}N$ values in consumer tissues can be used to infer the sources of carbon (energy) in food chains if the producer signatures (the isotopic baselines) are known. $\delta^{15}N$ values also show a stepwise increase with trophic level due to the tendency of animals to differentially excrete ^{14}N during digestion and assimilate ^{15}N during protein synthesis. The trophic position of consumers can be inferred above a known producer baseline (Bond & Jones 2010). The synthesis of different consumer tissues (e.g. blood, muscle, feathers, eggshell membranes) may involve different turnover rates (time periods) and variable fractionation patterns, which need to be considered when making inferences from stable-isotope data (Kelly 2000, Cherel *et al.* 2008, Bond & Jones 2010).

In marine ecosystems the carbon isotopic ratio ($\delta^{13}C$) in phytoplankton is determined by the availability of CO_2 for photosynthesis. During photosynthesis all plants preferentially fix the common lighter

^{12}C isotope within their tissues. However, where CO_2 is limited, a relatively high proportion of the heavier ^{13}C isotope is fixed, producing a larger or "enriched" δ^{13}C value in the resulting biomass. Sea temperature, vertical mixing, the rate of CO_2 fixation (i.e. productivity), and light or trace metal limitation all influence the amount of dissolved CO_2 available for photosynthesis in marine waters. As a consequence, phytoplankton living in warm, highly stratified and less seasonal tropical environments, with limited aqueous CO_2 levels, have relatively high δ^{13}C values compared with those from cooler, higher latitude waters. This effect produces a broad latitudinal gradient in δ^{13}C values across the oceanic basins (Bond & Jones 2010, Graham *et al*. 2010). Shallower, well-mixed and relatively productive inshore and shelf waters also tend to have more enriched δ^{13}C values than the adjacent oceanic waters. Dominant producers in the littoral zone, including macro-algae and seagrasses, have higher δ^{13}C values than phytoplankton. Carbon from these benthic systems may be exported into the pelagic food chains of the continental shelves. This "benthic–pelagic coupling" may also contribute to higher δ^{13}C values in the biota of inshore and shelf environments (Graham *et al*. 2010) than in the biota of oceanic ones.

The δ^{15}N values in marine producers such as phytoplankton depend on the fractionation of the nitrogen source. This is influenced by the various nitrifying and de-nitrifying transformations occurring through the nitrogen cycle. Inorganic (nitrate) nitrogen is relatively enriched in ^{15}N, producing high δ^{15}N values, which are also indicative of high nitrogen availability. Recycled (ammonia) nitrogen is less enriched in ^{15}N and recently fixed (N_2) nitrogen is depleted in ^{15}N. The δ^{15}N values therefore are a combined indicator of nitrate source, availability and uptake (Graham *et al*. 2010).

This paper uses carbon and nitrogen stable isotope analysis to build on existing knowledge of the foraging ecology of three dark tern species breeding in southwestern Australia and, in particular, of differences in their foraging habitats.

METHODS

This study uses the δ^{13}C and δ^{15}N signatures of feathers and eggshell membranes to investigate the foraging ecology of three dark tern species (Bridled Tern, Sooty Tern and Brown Noddy) with breeding colonies off the lower west coast of Western Australia (Fig. 1).

Feather keratin is laid down during the moult, and the δ^{13}C and δ^{15}N values in the protein structure capture a discrete foraging period coincident with feather growth. Once completed, feathers are inert structures that are not subject to tissue turnover (Cherel *et al*. 2008, Bond *et al*. 2009). Eggshell membranes are primarily composed of collagen (Yu Hung & Yu-Jie 2009). This protein is laid down in the oviduct during the latter stages of egg formation. It is not known whether there are any significant differences in stable isotope fractionation between keratin and collagen synthesis.

The sixth primary feather was extracted from adults to determine their stable isotope values from foraging during the nonbreeding
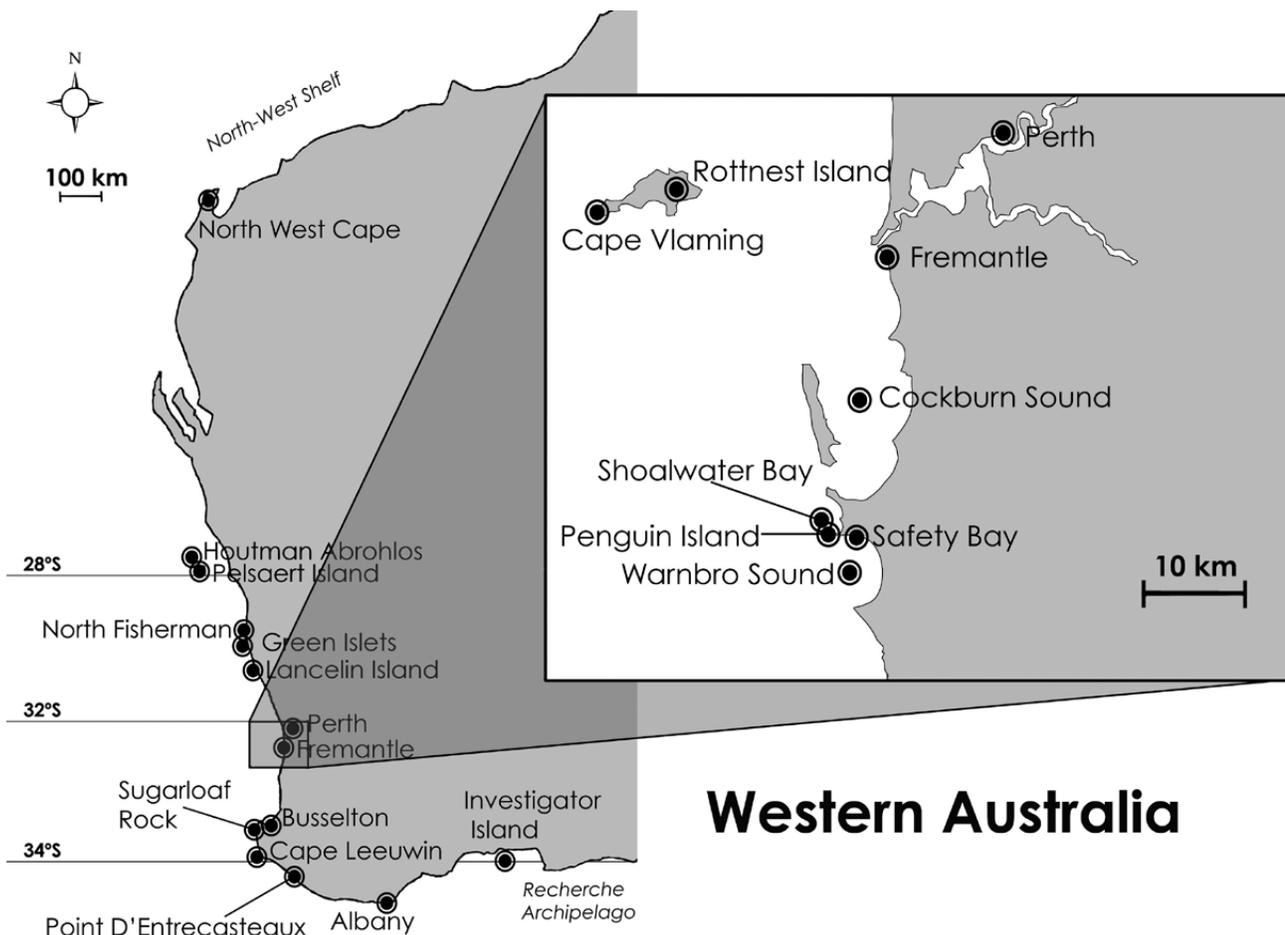

Fig. 1: Map of southwestern Australia showing location of study breeding colonies.

period. Samples from Bridled Terns were collected from the colony on Penguin Island (Fig. 1, Dunlop & Jenkins 1994, Dunlop 2009) late in the 2006/07 spring–summer breeding season (n = 5) and the 2008/09 season (n = 5). In the Bridled Tern new primaries typically erupt about 3 weeks after extraction (pers. obs.) during the breeding period and are completed within 9 weeks.

Adult feather samples from Brown Noddies were collected from incubating birds from the colony on Lancelin Island (Fig. 1, Dunlop 2005, Dunlop 2009) late in the 2006/07 spring–summer breeding season (n = 6) and the 2008/09 season (n = 5). Primaries (n = 10) were collected from recently dead adult Sooty Terns found at breeding colonies in the Easter Group of the Houtman Abrolhos Islands in December 2008.

Mesoptile down was collected from half-grown Bridled Tern chicks from the colony on Penguin Island in 2006/07 (n = 5) and 2008/09 (n = 7). Down was not retained on Noddy chicks of this age, so a secondary feather was selected. The feather samples from Noddy chicks were collected from the colony on Lancelin Island in 2006/07 (n = 4) and 2008/09 (n = 6). Recently hatched eggs with attached membranes were collected from the Bridled Tern colony on Penguin Island (n = 7) and the Brown Noddy colony on Lancelin Island (n = 5) in the 2006/07 season.

Prey samples were sorted from regurgitations collected during banding operations. The regurgitated gut contents from Bridled Terns tend to be heavily digested by comparison with those from noddies and Sooty Terns. The remains of Black-spotted Goatfish usually consist of empty head capsules and the characteristically tinsely skin and red-orange "Red Mullet" soft tissue. Regurgitate samples were collected from adult Bridled Terns feeding chicks at the Penguin Island colony in January and February 2010.

Samples of Beaked Salmon *Gonorhynchus greyi* (n = 6) and Anchovy *Engraulis australis* (n = 6) post-larvae were compiled from a number of intact individuals sorted from different regurgitated boluses. Fragments of Black-spot Goatfish *Parupeneus signatus* post-larvae were assembled into samples (n = 6) in the same way. These samples were then dried and frozen before grinding to a powder using a mortar and pestle. The samples were of whole dried fish.

Early in the breeding season Bridled Terns take small coastal forage fishes, including year 1 sardines or "pilchards" *Sardinops vagax* (Dunlop 1997). Sardines captured in the local fishery in 2004 were also analysed for their stable isotope signatures, and scales were used for the analysis of these adult fish to avoid the high lipid content of the muscle tissue.

Stable isotope analysis

The $\delta^{13}C$ and $\delta^{15}N$ values from feather and eggshell membrane samples collected in 2006/07 were analysed by Western Australian Biochemistry Centre. Samples collected later were analysed at the Natural Isotopes Laboratory at Edith Cowan University in Perth, Western Australia. There were no significant differences in $\delta^{13}C$ and $\delta^{15}N$ values for the equivalent tissues analysed by the two laboratories.

Feathers were cleaned of any extraneous materials, washed in deionised water and dried. The vascularised bases were removed from the Brown Noddy chick secondaries. The feathers were then chopped into small fragments using dissecting scissors before being powderised with stainless steel ball bearings in a centrifuge. Eggshell membranes were similarly washed and dried before being ground down to a powder.

Samples were weighed, placed in tin capsules and combusted by elemental analyser (ANCA-GSL, Europa, Crewe, United Kingdom) to N_2 and CO_2. The N_2 and CO_2 were then purified by gas chromatography, and the nitrogen and carbon elemental composition and isotope ratios determined by continuous flow isotope ratio mass spectrometry (20-20 IRMS, Europa, Crewe, United Kingdom). Reference materials of known elemental composition and isotopic ratios were interspaced with the samples for calibration.

Statistical analysis

Tables 1 and 2 summarize the collecting localities, tissue types, sample sizes and $\delta^{13}C$ and $\delta^{15}N$ values for the three tern species (Table 1) and four fish species (Table 2) sampled for stable isotope analysis. Mean $\delta^{13}C$ and $\delta^{15}N$ values between samples were compared using Student's *t*-test.

TABLE 1
Collecting localities, tissue types, sample sizes and values for $\delta^{13}C$ and $\delta^{15}N$
for the three tern species sampled for stable isotope analysis

Species (and collecting locality)	Tissue (and no. sampled)	$\delta^{13}C$ values			$\delta^{15}N$ values		
		Mean (SD)	Maximum	Minimum	Mean (SD)	Maximum	Minimum
Bridled Tern (Penguin Island)	Eggshell membrane (7)	-19.20 (0.35)	-18.87	-19.91	11.97 (0.68)	12.98	11.30
	Chick feathers (12)	-18.94 (0.39)	-19.44	-18.06	12.09 (0.39)	12.72	11.50
	Adult primary 6 (10)	-17.16 (0.47)	-16.62	-18.28	11.52 (0.62)	12.53	10.51
Brown Noddy (Lancelin Island)	Eggshell membrane (5)	-19.01 (0.402)	-18.72	-19.67	12.53 (0.17)	12.79	12.39
	Chick feathers (11)	-18.90 (0.16)	-18.62	-19.20	11.71 (0.63)	12.96	10.89
	Adult primary 6 (10)	-18.19 (0.52)	-16.81	-18.67	11.71 (1.05)	13.25	10.38
Sooty Tern (Albrolhos islands)	Adult primary 6 (10)	-16.26 (0.40)	-15.83	-17.04	12.63 (0.34)	13.34	11.94

RESULTS

There were no significant differences in the $\delta^{13}C$ and $\delta^{15}N$ values for samples of the same feathers collected in 2006/07 and 2008/09, so these results have been combined in the analysis (Fig. 2).

Similarly, there were no significant differences in either the $\delta^{13}C$ or $\delta^{15}N$ values in the eggshell membranes or chick feathers from Bridled Terns and Brown Noddies. However, the $\delta^{13}C$ of adult primary feathers of both species differed significantly from the feathers produced during the breeding season (Bridled Tern chick to adult $t = 3.42$, $P < 0.01$: Brown Noddy chick to adult $t = 3.0$, $P < 0.01$), by being relatively enriched in ^{13}C.

Both the $\delta^{13}C$ and $\delta^{15}N$ values from adult Sooty Tern primary feathers were significantly higher than those of the Bridled Tern (Bridled Tern — Sooty Tern primaries $\delta^{15}C$ $t = 3.91$, $P < 0.01$; $\delta^{15}N$ $t = 3.77$, $P < 0.01$) and Brown Noddy (Brown Noddy — Sooty Tern $\delta^{13}C$ $t = 5.75$, $P < 0.001$; $\delta^{15}N$ $t = 2.60$, $P < 0.01$).

The $\delta^{13}C$ or $\delta^{15}N$ values did not differ between the post-larval *Gonorhynchus* and *Engraulis* from Brown Noddy regurgitates. These were, however, significantly more enriched in both ^{13}C and ^{15}N than the undigested fragments of *Parupeneus* post-larvae collected from the Bridled Terns ($\delta^{13}C$ $t = 3.39$, $P < 0.01$; $\delta^{15}N$ $t = 2.37$, $P < 0.05$). The scale samples from coastally foraging sardines were enriched in ^{13}C with respect to all the post-larval prey types and significantly depleted in ^{15}N with respect to *Gonorhynchus/Engraulis* consumed by the Brown Noddies ($\delta^{15}N$ combined *Gonorhynchus/Engraulis* $t = 8.642$, $P < 0.001$).

DISCUSSION

Dark tern foraging ecology

The foraging ranges, and consequently marine habitats, of the dark terns are related to body size. The larger Sooty Terns and Brown Noddies forage at greater distances and in more oceanic environments than the smaller "outer shelf" foraging Bridled Terns and Lesser Noddies (Dunlop *et al*. 1988, Hulsman 1988, Dunlop 1997, Surman & Wooller 2003, Jaquemet *et al*. 2004, Ramos *et al*.

2006, Catry *et al*. 2009). Indeed, it could be argued that the guild subdivides into large and small dark terns.

Another related factor reducing potential competition within the guild is the strength of the commensal association with foraging sub-surface predators. Sooty Terns have an obligate relationship with epipelagic tuna *Tunnus* spp. (Jaquemet *et al*. 2004, 2007, Cherel *et al*. 2008), and Brown Noddies may also largely depend on the foraging opportunities these fish provide in the oceanic environment (Ramos *et al*. 2006). Lesser Noddies crowd the surface over foraging tuna (Hulsman 1988, Surman & Wooller 2003, Jaquemet *et al*. 2004) but also forage over less aggregated predators such as Dolphinfish *Coryphaena equiselis* (Jaquemet *et al*. 2004, 2007), Queenfish *Seriphus politus*, Spanish Mackerel *Scomberomorus maculatus* and Wahoo *Acanthocybium solandri* (pers. obs.).

The Bridled Tern has not been observed concentrating over predatory fish in large numbers, although small groups may gather fleetingly over "bait boils," often in association with Wedge-tailed *Puffinus pacificus* and Little *P. assimilis* shearwaters (Dunlop 1997). The Bridled Tern appears to have a facultative association with predatory fish, utilising foraging schools of predatory fish in the absence of interference competition from seabirds that can monopolise the water surface (Hulsman 1988, Dunlop 1997).

Bridled Terns take a diverse range of larval, post-larval and immature fish and crustacean prey species associated with rafts of floating *Sargassum*, which are common on the Western Australian continental shelf during most of the breeding season. Typically the "windrows" of macro-algae, and the associated Sargasso-fauna communities, are concentrated in the down-welling zones created by persistent wind stress (Langmuir cells) or by tidal or temperature fronts (Dunlop 1997).

Analysis of stable isotope values

Beaked Salmon post-larvae make up 78% by volume of the dietary intake of Brown Noddies in the region during successful breeding seasons (Surman & Nicholson 2009). The $\delta^{15}N$ values for both the Brown Noddy eggshell membranes and chick feathers are one trophic level (2.59‰, Bond *et al*. 2009) above those of

TABLE 2
Collecting localities, tissue types, sample sizes and values for $\delta^{13}C$ and $\delta^{15}N$
for the four prey fish species sampled for stable isotope analysis

Species (collecting locality)	Tissue (and no. sampled)	$\delta^{13}C$ values			$\delta^{15}N$ values		
		Mean (SD)	Maximum	Minimum	Mean (SD)	Maximum	Minimum
Parupeneus signatus post-larvae (Penguin Island)	Entire larvae (6)	-20.8 (0.578)	-19.81	-21.41	7.36 (0.188)	7.67	7.17
Gonorhynchus greyi post-larvae (Lancelin Island)	Entire larvae (6)	-19.73 (0.099)	-19.87	-19.62	9.59 (0.354)	10.31	9.35
Engraulis australis post-larvae (Lancelin Island)	Entire larvae (6)	-19.64 (0.285)	-19.29	-19.95	9.68 (0.232)	10.10	9.43
Sardinops vagax (Fremantle purse-seine fishery)	Scales (6)	-17.82 (0.12)	-17.70	-17.94	7.93 (0.06)	8.00	7.85

their dominant prey species (Fig. 2). This is expected, given the dominance of this prey type in the Brown Noddy's diet.

While the δ^{13}C and δ^{15}N values from the Bridled Tern eggshell membranes and chick feathers appear to indicate a foraging environment similar to that of the Brown Noddy, there is a major discrepancy between the isotopic values in the tissues of *Parupeneus* post-larvae and the expected fractionation in the tissues of its predator (Fig. 2). *Parupeneus* post-larvae were found in 31.4% of Bridled Tern regurgitate samples examined by Dunlop (1997); however, estimation of volume was not feasible because most samples were highly digested. The Bridled Tern's diet is much more diverse than that of the Brown Noddy in this region and is known to include a range of small predatory fish and crustaceans associated with the *Sargassum* rafts (Dunlop 1997). The mean trophic level of the Bridled Tern's diet during the breeding season is therefore likely higher than that indicated by the tissues of the Black-spotted Goatfish post-larvae.

The Black-spotted Goatfish/Anchovy post-larvae consumed by the Brown Noddies were significantly enriched in both ^{13}C and ^{15}N compared with *Parupeneus*. This indicates that the Brown Noddies are foraging in areas with relatively elevated levels of inorganic nitrogen and productivity in comparison with foraging areas of Bridled Terns. Given the foraging range of the Brown Noddy, these areas could be small, currently unidentified, shelf-edge upwellings or warm core eddies in the Leeuwin Current. Published δ^{13}C values for particulate organic matter (Hanson *et al.* 2005) and larval fish (Waite *et al.* 2007) in Leeuwin Current structures of the adjacent deep ocean are more depleted in ^{13}C than those found in the Beaked Salmon/Anchovy post-larvae consumed by the Brown Noddies. This suggests that their foraging area is closer to the coast and likely associated with a relatively nutrient-enriched shelf-edge feature. By comparison, the δ^{13}C and δ^{15}N values of the sardines (Fig. 2) indicate a more coastal prey species (enriched ^{13}C) in a nitrate-deficient (depleted ^{15}N) environment.

The δ^{13}C and δ^{15}N values from the Black-spotted Goatfish post-larvae suggest that Bridled Terns forage in relatively oligotrophic and unproductive environments. Such conditions are typical of much of the southwestern Australian continental shelf (Feng *et al.* 2009). The ability of Bridled Terns to utilise relatively unproductive environments may reduce competition with other dark terns, particularly the Lesser Noddy.
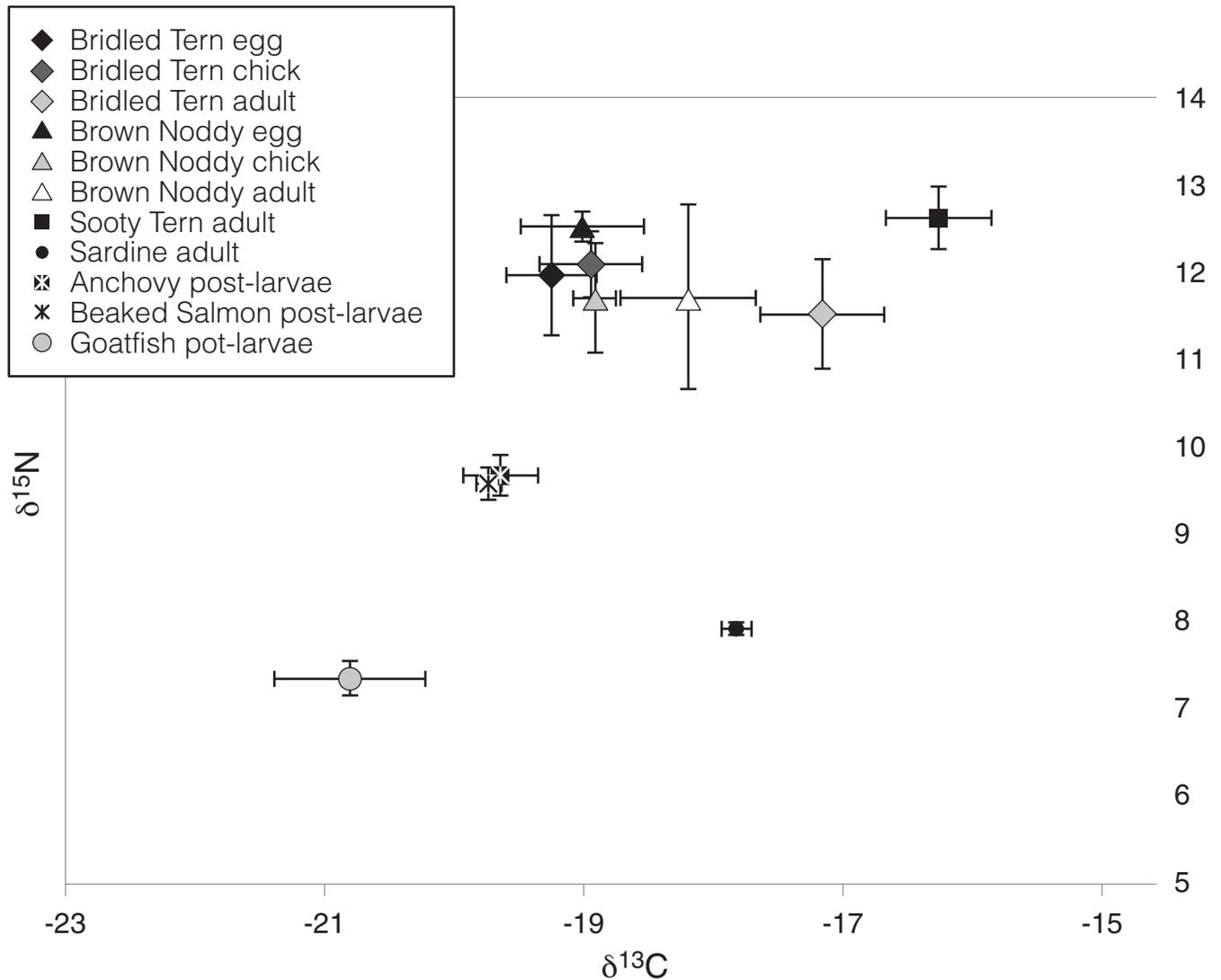

Fig. 2: Values of δ^{13}C and δ^{15}N for dark tern eggshell membranes, chick feathers and adult primaries from breeding colonies in southwestern Australia. Also shown are the δ^{13}C and δ^{15}N values from the main fish prey species for these tern species. Symbols represent means, with error bars representing standard deviation.

Bridled Terns breeding on islands of southwestern Australia spend the austral winter in the northwest Sulawesi Sea between about 4°N and 7°N (Dunlop & Johnstone 1994), where they undergo the basic moult. The high $\delta^{13}C$ value in the adult primaries relative to the chick feathers from the breeding area reflects the relative enrichment in ^{13}C of tropical low-latitude waters. Its larger congener, the Sooty Tern, has higher $\delta^{13}C$ and $\delta^{15}N$ values in its primary feathers. This almost certainly reflects the Sooty Terns' tendency to forage over relatively productive water masses (Jaquemet *et al.* 2007) rather than any difference in latitude. Tuna also aggregate in such areas, providing foraging opportunities for Sooty Terns. Again, Bridled Terns appear to be foraging over less productive waters, in this case in the wintering area, than other dark terns.

The $\delta^{13}C$ values in the primary feathers of adult Brown Noddies confirms that they occupy lower latitude waters outside the breeding season, but these waters are not as close to the equator as those occupied by the Bridled or Sooty Terns. Detailed $\delta^{13}C$ "isoscapes" are not yet available for the eastern Indian Ocean, but Brown Noddies breeding off southwestern Australia likely winter closer to the subtropics.

ACKNOWLEDGEMENTS

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