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The nutritional nexus: linking niche, habitat variability and prey composition in a generalist marine predator

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Keywords: niche theory, multidimensional nutritional niche framework, nutritional landscapes, multivariate ellipse-based Bayesian approach, bio-logging, seabirds.

Summary

1. Our understanding of the niche concept will remain limited while the quantity and range of different food types eaten remains a dominant proxy for niche breadth, as this does not account for the broad ecological context that governs diet. Linking nutrition, physiology and behaviour are critical to predict the extent to which a species adjusts its nutritional niche breadth at the levels of prey ("prey composition niche", defined as the range of prey compositions eaten), and diet ("realized nutritional niche" is the range of diets composed through feeding on the prey).
2. Here we studied adult-chick rearing Australasian gannets (*Morus serrator*) to propose an integrative approach using sea surface temperature anomalies (SSTa), geographic location and bathymetry over different years, to explore their relationship with the nutritional composition of prey and diets (i.e., prey composition and nutritional niche breadth), habitat use and foraging behavior.
3. We found that gannets feed on prey that varied widely in their nutritional composition (have a broad prey composition niche), and composed diets from these prey that likewise varied in composition (have a broad realized nutritional niche), suggesting generalism at two levels of macronutrient selection.

4. Across seasons, we established “*nutritional landscapes*” (hereafter *nutriscapes*), linking the nutritional content of prey (wet mass protein to-lipid ratio -P:L-) to the most likely geographic area of capture and bathymetry. *Nutriscapes* varied in their P:L from 6.06 to 15.28, over time, space and bathymetry (0 to 150 m).
5. During warm water events (strong positive SSTa), gannets expanded their foraging habitat, increased their foraging trip duration and consumed prey and diets with low macronutrient content (wet mass proportions of P and L). They were also constrained to the smallest prey composition and realized nutritional niche breadths.
6. Our findings are consistent with previous suggestions that dietary generalism evolves in heterogeneous environments, and provide a framework for understanding the nutritional goals in wild marine predators and how these goals drive ecological interactions and are, in turn, ultimately shaped by environmental fluctuations.

Introduction

The niche concept is a powerful tool in ecological and evolutionary theory. However, niche definitions can be vague and there are often difficulties in measuring and characterizing niches (Pulliam 2000; Kearney 2006; Newsome *et al.* 2007). Niche breadth, in particular, has been frequently linked to dietary generalism and is often characterized in terms of food types ingested and/or their energy content (Futuyma & Moreno 1988). Thus, it is widely believed that generalists consume a wide variety of foods and have a wide niche, whereas specialists consume a narrow range of foods and have a narrow niche (Ducatez, Clavel & Lefebvre 2015). However, the nutritional implications of niche breadth are seldom considered in the application of niche theory. This is an important omission, because nutrients provide the mechanistic link between an animal's foraging choices and fitness, and are therefore

indispensable for understanding the distributions of animal populations (Raubenheimer, Simpson & Tait 2012).

Nutritional ecology provides a flexible context for understanding the intricate interactions between organisms and their nutritional environment (Parker, Barboza & Gillingham 2009; Raubenheimer, Simpson & Mayntz 2009). A conceptual and analytical framework from nutritional ecology called nutritional geometry (NG) has enabled scientists to gain a new ecological perspective of nutrition by simplifying the complexities of modelling foods (hereafter prey) in relation to foraging behaviour, physiology and geographic processes (Raubenheimer & Simpson 1993; Raubenheimer 2011). Recently, NG was used to develop a multidimensional nutritional niche framework (MNNF) to unify food choices and diet composition into a multi-level classification of dietary generalism (Machovsky-Capuska *et al.* 2016a). This novel approach allows the characterization of niche breadth *via* the macronutrient composition of diets that can sustain a population (i.e. their realized nutritional niche), and the range of prey compositions (“prey composition niche”) and physical and ecological attributes of prey that a population can exploit (i.e. their food exploitation niche).

It has been suggested that nutritional niche breadth is shaped by several non-exclusive factors. First, in order to meet potentially changing nutritional requirements, foragers must adjust their foraging behaviour to select combinations of prey available to provide the target mix of nutrients (Machovsky-Capuska *et al.* 2016b). Second, the location and quality of foods are likely to influence prey consumption and foraging decisions (Spitz *et al.* 2012; Machovsky-Capuska *et al.* 2014). Third, interactions between bathymetry, physical and biological processes promote nutrient-rich environments with high prey quality (Hunt *et al.* 1998). Fourth, environmental fluctuations influence the habitat in which a population can forage and subsist (Costa 2007; Carroll *et al.* 2016), for example variation in sea surface temperature (Montevecchi & Myers 1997; Perry *et al.* 2005). Former dietary niche

characterizations have been hampered by inadequate consideration of these complex factors. The MNNF approach, however, attempts to place diet in the context of these variables, thus contributing to a better understanding of the constraints and opportunities that influence diet breadth in animals.

Marine apex predators are long-lived species that forage in complex three dimensional environments, and therefore represent an ideal group to better understand dietary generalism in the wild (Österblom *et al.* 2008; Spitz *et al.* 2011, 2012; Malinowski & Herzing 2015; Machovsky-Capuska *et al.* 2016c; Denuncio *et al.* 2017). Understanding the foraging goals of marine predators is pivotal to predicting how they will respond to environmental changes in prey availability and composition (Tait *et al.* 2014). Although habitat use is a central aspect of foraging, marine ecologists often study foraging behaviour in isolation, without addressing the multiple variables and scales that shape their environments (Austin *et al.* 2006). Gannets (*Morus* spp.), in particular, have been extensively studied with respect to both their foraging behaviour and food preferences. Based on the diversity of prey they consume, gannet dietary patterns have often been described as generalist, opportunistic or flexible feeders (Bunce & Norman 2000; Lewis *et al.* 2003; Montevecchi 2007; Wanless *et al.* 2008; Ropert-Coudert *et al.* 2009; Machovsky-Capuska *et al.* 2014). Although a few studies have highlighted the importance of prey quality in different gannet populations (Bunce 2001; Grémillet *et al.* 2008; Tait *et al.* 2014), the extent to which gannets are dietary generalists or specialists in terms of the foods that they exploit and diets that they compose from those foods remains to be established.

Here we combine niche theory and nutritional geometry, with data from Global Positioning System (GPS) data loggers, dietary analysis, macronutrient composition of prey and diets with a multivariate ellipse-based Bayesian approach to characterize the prey composition niche and realized nutritional niche of Australasian gannets (*M. serrator*;

hereafter gannets). Specifically, we addressed the following questions: i) To what extent does the nutritional composition of prey and of diets vary spatially and temporally?; ii) Do gannets adjust their foraging behaviour in regards to the macronutrient composition of prey, and iii) Do environmental factors (in this case Sea Surface Temperature anomalies (SSTa) and bathymetry) influence nutritional composition of prey, foraging behaviour and habitat use?

Material and methods

Study area

Fieldwork was conducted on Farewell Spit (FS, New Zealand, 40°33'S, 173°01'E), during the 2 to 5-week-old chick-rearing period in December and January 2011-2012, 2013-2014, 2014-2015 and 2015-2016. FS is a beach colony located at sea level with a population of gannets estimated at 3,900 breeding pairs (Schuckard *et al.* 2012).

Nutritional composition of prey and diets and niche breadth

Adult gannets captured using a blunt-tip shepherd's crook, were banded with an individually numbered metal ring on their leg and a unique mark on their chest using non-toxic Sharpie markers ©. These techniques enabled us to capture and track always different individuals. Birds were handled for <10 min, and soon after released at the edge of the colony. This study was conducted under Sydney Animal Ethics Committee (N00/7-2013/3/6016), Massey University Animal Ethics Committee (13/65) and the New Zealand Department of Conservation (35189-FAU).

Regurgitations were collected from different individuals over four breeding seasons (2011-2012 $n=24$, 2013-2014 $n=35$, 2014-2015 $n=51$, and 2015-2016 $n=64$). As gannets are known for transporting recently captured undigested prey in their proventriculus, we collected regurgitations as soon as they returned from foraging to the colony (Machovsky-

Capuska *et al.* 2011a) reducing the loss of prey macronutrient and water content (Montevecchi & Piatt 1987). Samples were collected from spontaneous regurgitations or after a 30 sec throat massage during handling, and stored in individual polythene bags at -20 °C within five hours of collection.

Samples were defrosted, individual prey items were weighed to 0.1 g and the total length measured to 0.1 mm prior to taxonomic identification using published guides (Paulin *et al.* 1989). Following Duffy and Jackson (1986), we calculated: i) the mass contribution of each prey items to the total diet as a mass percentage (M%), ii) the percentage of the total number of prey item contributed by individuals of a particular species as a numerical abundance percentage (N %), and iii) the percentage of gannets that had a particular species in their diet as a frequency of occurrence percentage (F %).

We followed the methodology established by Tait *et al.* (2014) and only selected prey for proximate composition analyses with the following characteristics: a) undigested prey samples and b) from the most representative prey items that contributed > 1% (wet mass) to the diets of gannets. Given that carbohydrate content is a minimal nutritional component of most marine prey (Craig, Kenley & Talling 1978) and fresh water is only available to seabirds from food moisture (Montevecchi & Piatt 1987), the proximate composition analysis and our comparisons are based on three essential nutrients: protein (P), lipid (L), and moisture (hereafter water -W-). All samples were oven-dried at 60° C, ground to powder with a laboratory mill and then weighed before laboratory analysis. Protein (estimated as Nitrogen x 6.25) was determined using the Kjeldahl procedure (see AOAC 2005 for more details). The method of Mojonnier was used to measure total lipid (hereafter lipid, AOAC 2005). W was estimated by drying the samples in a convection oven at 125°C and combining the water loss with the initial loss from the overnight dry-down (AOAC 2002). Ash was determined by ignition in a furnace at 550 °C (AOAC 2005).

Under the MNNF (Machovsky-Capuska *et al.* 2016a) we linked a well-established proportions-based approach (right-angled mixture triangle -RMT-) that enables the modelling of nutritional niches (Raubenheimer 2011) with a multivariate ellipse-based Bayesian approach that generates Standard Ellipses Areas (SEA) to measure isotopic niches breadth from proportions (Jackson *et al.* 2011). Following Syväranta *et al.* (2013), in order to account for small sample sizes, we used corrected versions of SEA (SEAc). Hence, this integrative approach was used to measure realized nutritional niche and prey composition niche breadths (SEAc).

Foraging behaviour

Global Positioning System (GPS) data loggers were deployed on different individual adult chick-rearing gannets during three breeding seasons (2011/2012 n=11, 2014/2015 n=17 and, 2015/2016 n=11). Departing birds were captured immediately after adopting the sky-pointing posture for data logger deployments, as described in Machovsky-Capuska *et al.* (2014). Canmore GT-730FL-S (Taiwan) GPS loggers embedded in a Loksak® waterproof bag (Loksak, USA) weighing 45g, were attached with Temflex 1610 tape to the four central tail feathers. Following Machovsky-Capuska *et al.* (2014), loggers were programmed to record data related to position (latitude, longitude, and altitude), speed and time at 1-sec intervals. Marked birds were recaptured upon arrival at the colony after one foraging trip, and loggers and tape strips were retrieved.

Gannet GPS data were speed filtered following McConnell, Chambers and Fedak (1992) (removal of points >75 km/h), and standardized to a 2 second interval between points (minimum interval observed in data; season 2011-2012), prior to analysis. Individual foraging trips were extracted using BirdLife International's '*marine IBA*' R package (Lascelles *et al.* 2016). Previous studies have shown that gannet dive durations are primarily between 3-

8 sec (Machovsky-Capuska *et al.* 2011b, 2012); in this study dive locations were inferred from interruptions of between 3-8 sec in GPS signals from our high resolution loggers since interruptions exceeding > 10 sec are likely to be related to loss of satellite signal reception (Pichegru *et al.* 2007; Machovsky-Capuska *et al.* 2011b, 2014; Moseley *et al.* 2012). Using the GPS data, we calculated a range of movement parameters for each foraging trip including maximum distance away from the colony (MDC), total foraging path (TFP) and foraging trip duration (FTD). To investigate foraging behaviour, we applied Hidden Markov Models (HMM) to the GPS data. We constructed a single HMM for each year of GPS tracking, including an identifier for each trip, using the package 'moveHMM' (Michelot, Langrock & Patterson 2016). For each consecutive GPS point, the step length and turning angle were calculated, producing three distributions consistent with resting (slow sinuous movement), foraging (medium speed sinuous movement) and transiting (fast directed movement) behaviours observed in HMM studies of Sulids (Boyd *et al.* 2014; Oppel *et al.* 2015). The fitted HMMs were then used to classify each GPS point as either: foraging, resting or transiting, and from this we calculated the foraging time (FT) and transiting time (TT) of each trip (Miller *et al.* 2017). For each gannet, we defined the general use foraging area by estimating the 95% utilization distribution (UD 95) and the prey capture area by obtaining the 50% utilization distribution (UD 50) from kernel analysis of their dive locations (Worton 1987). Kernels were constructed and linked with bathymetry in the package 'adehabitat HR' (Calenge 2006) with a grid size of 0.5 km and a smoothing parameter (h) of 5 km, identified as the most appropriate area-restricted search scale (Lascelles *et al.* 2016).

Sea surface temperature and bathymetry

Satellite-derived Sea Surface Temperature (SST, MODIS-Aqua) at a resolution of $0.01^\circ \times 0.01^\circ$ were obtained from Giovanni data portal (<http://giovanni.gsfc.nasa.gov/giovanni/>).

Monthly SST was acquired within 4 km of FS colony from December 2006 to December 2016. We obtained the mean SST during December-January of each season (2011-2012: 18.1 ± 0.3 ; 2013-2014: 17.9 ± 0.6 ; 2014-2015: 18.7 ± 0.0 and 2015-2016: 19.2 ± 1.3) compared with the 10 years December-January SST mean ($18.3 \pm 1.0^{\circ}\text{C}$) to establish potential warmer or colder anomalies (SSTa) in the gannet's foraging area. We also accessed bathymetry measurements from the New Zealand 250m gridded bathymetric dataset using the National Institute of Water and Atmospheric Research (NIWA) website (<https://www.niwa.co.nz/our-science/oceans/bathymetry>).

Nutritional landscapes

For each of the tracked gannets that regurgitated upon logger retrieval (2011-2012, $n=3$; 2014-2015, $n=8$; 2015-2016, $n=10$), we established “*nutritional landscapes*” (hereafter *nutriscapes*), linking the nutritional content of prey (wet mass protein to-lipid ratio -P:L-) to the most likely geographic area of capture and bathymetry. First, considering gannets' overall high success in prey capture (72%, Machovsky-Capuska *et al.* 2011a, 2012), we linked each individual's area of capture from dive locations (UD 50, estimated above) with the average wet mass P:L ratio of prey items caught during foraging trips. Second, we then mapped all UD 50s from each sampling year together to identify main *nutriscapes* and their nutritional composition. If UD 50s from one or more gannets overlapped, we assigned the mean nutritional value to that *nutriscap*e (see Supplementary information for codes).

Data analysis

All analyses were performed in the statistical software environment program R version 3.2.4 (R Core Team 2016). Linear and Generalized linear models (LMs and GLMs) were implemented using the ‘*lm*’ and ‘*glm*’ functions and Linear mixed models (LMMs) were

performed with ‘*lme4*’ package (Bates *et al.* 2015). Data analysed using LMs were initially tested using Levene’s test for homoscedasticity and Shapiro-Wilk’s test for normality.

Inter-annual differences were evaluated by fitting a 4-level categorical predictor denoting the season in which observations were made in LM/GLM. Evaluating differences in the total number of prey items brought to the colony between seasons, we used a quasi-poisson (log-link) GLM where the response was the count of each prey species regurgitated by an individual. Variations in weight and length between seasons of prey species were evaluated using LMs. Weight and length of prey were log-transformed and fitted against the categorical predictor for season.

Following Machovsky-Capuska *et al.* (2016b), linear mixed models (LMMs) were used to evaluate the between-species variation (quantified as standard deviation, -SD-) in the proximate composition of prey. The LMM were implemented with the ‘*lmer*’ function in the package ‘*lme4*’ (Bates *et al.* 2015) and fitted the logit transformation of the wet mass proportions of P, L, W, and log ratio of the proportion of protein to lipid (lnPL) from each individual prey item, with species ID as a random effect. The statistical significance of between-species variance was assessed using a likelihood ratio test with the ‘*rand*’ function in the package ‘*lmerTest*’ (Kuznetsova *et al.* 2015).

To explore whether the nutritional composition (log wet mass proportion of P, L and lnPL and W) of diets fluctuated over seasons, we fitted a LMs with the nutritional composition of interest (as per above) from each diet sample as the response. Seasonal differences in SEAc were estimated via Bayesian interference (SEAb) using Markov chain Monte Carlo simulation with 10^4 iterations with 95% credible intervals (CI) among groups (Jackson *et al.* 2011). Following Pelletier *et al.* (2014), this method enables direct interpretations of the differences in SEAb that we tested using LM.

Seasonal differences in habitat use and foraging behaviour parameters were evaluated by fitting an LM with a 3-level categorical predictor for each season. Following Bonett and Wright (2000), we performed Pearson correlations to explore possible seasonal relationships between niche breadths (SEAc) with habitat use (UD50 and UD95) and foraging behaviour (TFP and FTD).

Bathymetry differences between seasons were tested using LM. To assess the influence of SSTa on foraging behaviour, habitat use parameters and nutritional composition of prey (as described previously), LMs were used. Here each outcome was fitted against the SSTa of the time at which the observation was made (binary predictor; colder or warmer than the 10 years mean). MDC, FTD, Total dive duration were log (natural) transformed to ensure the data was normally distributed.

Nutritional niche breadths were calculated using SIBER package (Stable Isotope Bayesian Ellipses) in R version 3.2.4. We report parametric data as mean \pm standard error (SE) unless otherwise stated. For among-season differences in outcomes, we present overall effects from LMs/GLMs.

Results

Nutritional composition of prey, diets and niche breadth

A total of 172 regurgitations were collected over four breeding seasons (Table 1). A total of 1341 prey items were identified from these samples, including eight species of fish kahawai (*Arripis trutta*), barracouta (*Thyrsites atun*), garfish (*Hyporhamphus ihi*), yellow eye mullet (*Aldrichetta forsteri*), yellow tail jack mackerel (*Trachurus* spp.), pilchard (*Sardinops neopilchardus*), saury (*Scomberesox saurus*) and anchovy (*Engraulis australis*), and arrow squid (*Nototodarus* spp.). From the total number of regurgitations, 84.9% contained only one

species of prey, 13.4% contained two species and 1.7% contained three species. Prey items had a mean weight of 22.4 ± 1.1 g and a mean length of 13.4 ± 0.2 cm.

From all the prey species, garfish had the highest wet mass P:L ratio (21.4:1.0) whereas barracouta had the lowest P:L ratio (1.5:1.0, Figure 1). The nutrient composition of the different prey species consumed by gannets showed differences in the wet mass proportions of P (estimated between-prey species $SD = 0.12$, $\chi^2 = 22.7$, d.f. = 8, $P < 0.0001$), L (estimated between-prey species $SD = 0.64$, $\chi^2 = 10.5$, d.f. = 8, $P < 0.001$), the lnPL (estimated between-prey species $SD = 0.74$, $\chi^2 = 11.5$, d.f. = 8, $P < 0.0001$) and W (estimated between-prey species $SD = 0.03$, $\chi^2 = 53.8$, d.f. = 8, $P < 0.0001$). The SEAc: 9.19 combined with the wide range of P:L wet mass ratios in the prey consumed over four breeding seasons (from 1.5:1.0 to 21.4:1.0) provide an estimate of breadth of the prey composition niche (Figure 1). The realized nutritional niche breadth was also estimated by combining SEAc: 4.65 and the P:L wet mass ratios from the diets of gannets (from 1.5:1.0 to 15.2:1.0) (Figure 1).

The number of prey items per foraging trip was significantly different between years (GLM, $F_{3,1337} = 15.41$, $P < 0.0001$), with the greatest number observed in 2015-2016 (see Supplementary information Table S1). The weight and length of prey items consumed by gannets differed significantly between seasons (LM weight, $F_{3,1337} = 45.08$, $P < 0.05$ and LM length, $F_{3,1337} = 55.27$, $P < 0.05$), with the lightest and smallest consumed in 2015-2016 (see Supplementary information Table S1). The greater number of prey eaten in 2015-2016 did not, however, compensate for their smaller size, as meal sizes were significantly lighter in 2015-2016 than in other years (LM, $F_{3,168} = 54.33$, $P < 0.05$, see Supplementary information Table S1). Inter-annual differences of the nutritional composition of diets were significant for the wet mass proportion of P (LM, $F_{3,168} = 20.63$, $P < 0.0001$), L (LM, $F_{3,168} = 23.14$, $P < 0.0001$), W (LM, $F_{3,168} = 5.35$, $P < 0.001$) and lnPL (LM, $F_{3,168} = 27.71$, $P < 0.0001$).

Differences between years were also observed in the breadth dimensions of the prey composition niches (LM, $F_{3,15996} = 29230$, $P < 0.0001$) and the realized nutritional niches (LM, $F_{3,15996} = 50710$, $P < 0.0001$) (Figure 2, also see Supplementary information Table S2).

Foraging behaviour

A total number of 39 foraging trips were collected from birds carrying GPS data loggers (Table 2). The foraging habitat ranged from 1100.89 to 1374.24 km² for UD95 and from 222.54 to 273.05 km² for UD50 (Table 2), with no difference detected between breeding seasons (UD 50, LM, $F_{2,36} = 0.95$, $P = 0.33$ and UD 95, LM, $F_{2,36} = 2.04$, $P = 0.16$) (Table 2).

The mean MDC that gannets travelled away from the colony was 56.1 ± 4.5 km (Table 2). Gannets showed the longest FTD in 2015-2016 (LM, $F_{2,36} = 4.60$, $P < 0.05$) and spent almost 25% more time foraging (LM, $F_{2,36} = 6.16$, $P < 0.01$) in deeper areas than during other study years (LM, $F_{2,36} = 5.82$, $P < 0.01$). Total dive duration showed that longest dives were recorded in 2011-2012 (LM, $F_{2,36} = 3.42$, $P < 0.05$). No significant differences between seasons were observed in the MDC (LM, $F_{2,36} = 1.31$, $P = 0.28$) and in the TFP (LM, $F_{2,36} = 0.42$, $P = 0.66$) (Table 2). Although non-significant, negative seasonal trends were found between realized nutritional niche breadths with foraging behaviour and habitat use parameters (SEAc and UD50, Pearson $r = -1.00$, $P < 0.05$, $n = 6$; SEAc and UD95, Pearson $r = -0.81$, $P = 0.40$, $n = 6$; SEAc and TFP, Pearson $r = -0.98$, $P = 0.13$, $n = 6$ and SEAc and FTD, Pearson $r = -0.93$, $P = 0.24$, $n = 6$).

Sea surface temperature anomalies

Strong negative indices (colder water than average) were recorded in 2013-2014 (December-January: -0.5 °C) and 2011-2012 (December-January: -0.3 °C), whereas strong positive

values (warm water than average) were recorded in 2014-2015 (December-January: +0.4 °C) and 2015-2016 (December-January: +0.9 °C).

Foraging behaviour and habitat used were influenced by SSTa. During warmer water periods (positive SSTa) gannets increased their foraging habitat UD95 (km²), maximum distance to the colony (km), foraging trip duration (h), foraging path length (km), transiting and foraging times (h) and bathymetry depth preference (m), whereas during colder water periods (negative SSTa) gannets showed a significant increase in total dive duration (s) (Table 3). SSTa also influenced the nutritional composition of prey and diets consumed by gannets. During colder water periods (negative SSTa), prey species and gannet diets revealed higher wet mass proportions of P and L and lower lnPL than in warmer periods (positive SSTa, Table 4).

Nutritional landscapes

The nutriscaes varied in the nutritional composition of prey, geographic location and bathymetry over the seasons studied. The wet mass P:L ranged from 7.26 to 13.0 in 2011-2012, 6.06 to 15.28 in 2014-2015, and 6.50 to 11.52 in 2015-2016. Gannets dived predominantly in shallow waters (0-50 m) during 2011-2012, moving to deeper areas (50-100m) in 2014-2015 and in 2015-2016 (50-150m) (Figure 3).

There were no differences between tracked birds with and without regurgitations in MDC (LM, $F_{1,37}= 1.66$, $P= 0.20$), FTD (LM, $F_{1,37}= 1.57$, $P= 0.48$) and bathymetry (LM, $F_{1,37}= 1.40$, $P= 0.24$), suggesting that the nutriscaes proposed for each breeding season are representative for the wider tracked population. However, as a consequence of lower sample size of tracked birds that regurgitated, the UD50 of nutriscaes did not fully overlap with the UD50 of the wider tracked population (Figure 3).

Discussion

A mechanistic understanding of the species' niche, including physiology and especially behaviour, is critical to predict how they will adjust to novel circumstances such as environmental fluctuations (Kearney 2006). A useful and robust measure of dietary niche shape and breadth should contemplate the following factors: i) the range of prey consumed; ii) the evenness of prey components in the diet over time and iii) foraging behaviour and geographic location (Bearhop *et al.* 2004) and iv) nutritional composition of prey and diets; and v) the influence of environmental fluctuations (e.g. SSTa) (Machovsky-Capuska *et al.* 2016a). Accordingly, our study yielded several novel insights into the nutritional niche of gannets at different scales. First, we characterized the prey composition and the realized nutritional niches and provide evidence of their seasonal fluctuations in shape and breadth (criteria i, ii and iv above). Second, we demonstrated the importance of linking foraging behaviour and the influence of environmental conditions (SSTa) with nutritional niche theory (criteria iii and v).

Measuring nutritional niches

The ecological niche concept has been fundamental to ecology since its development fifty years ago (Chase & Leibold 2003). Although considerable effort has gone into defining, measuring and quantifying the ecological niche, the concept remains poorly characterized (Feinsinger, Spears & Poole 1981; Kearney 2006; Kearney *et al.* 2010). While nutritional niches have often been described using carbon and nitrogen either in the form of isotope ratios (Newsome *et al.* 2007) or concentrations in food items (González *et al.* 2017), the biological and physiological assumption that these concentrations are surrogate of lipids, proteins and carbohydrates may often be incorrect (Raubenheimer, Simpson & Mayntz 2009; Wilder & Eubanks 2010).

A growing body of evidence suggests that vertebrate predators consume prey that vary in their nutritional and energetic compositions (Mayntz *et al.* 2009; Lenky *et al.* 2012; Malinowski & Herzing 2015; Machovsky-Capuska *et al.* 2016c, d). Here we demonstrated that there is an appreciable variation in the proportional wet mass contribution of P, L, W and PL ratio in the prey species consumed by gannets, which is consistent with previous findings on gannet prey species (Tait *et al.* 2014; Machovsky-Capuska *et al.* 2016b). These results further support previous suggestions on the importance of nutrient content rather than just energetic value of prey (Machovsky-Capuska *et al.* 2016d). As expected, the differences in the nutritional values of prey were then translated into seasonal fluctuation in the breadth (SEAc) of both the prey composition niche and realized nutritional niche.

As a best practice to characterize and measure prey composition and realized nutritional niches, we suggest the use of SEAc combined with nutritional ratios. However, as is generally true of measuring niches in wild populations (Chase & Leibold 2003; Raubehneimer *et al.* 2015), careful consideration needs to go into sampling design, including how diet is measured, and the sampling effort required to make reliable estimates of diet breadth. There is no simple answer to these questions; each needs to be addressed in relation to the details of particular study systems and research aims.

In our study, we were able to measure diet by soliciting regurgitations from parent birds when they returned to the nest from foraging. A peculiarity of this method is that regurgitations can combine foods that would contribute to the diet of the parents with those that would be provisioned to chicks (Ropert-Coudert *et al.* 2004). There is no easy way of distinguishing these, and consequently the use regurgitations can be problematic in studies that aim to assess the dietary composition of reproducing adults or of their chicks. The use of regurgitations does not, however, compromise studies that aim to enumerate dietary niches. This is because the niche concept refers to the resources required to maintain the population,

including all stages of the life cycle (Pulliam 2000). Indeed, sampling regurgitations that might have consisted of both adult and chick foods was a benefit in our study, because this approach efficiently encompasses the diets of both stages of the life cycle.

The question of sampling effort is particularly relevant to demonstrating that a species is a dietary specialist. To establish dietary specialism, it would need to be demonstrated that the range of foods eaten is not an artefact of local or otherwise insufficient sampling, but rather a true reflection of the species' biology. This could be done either by ensuring that sampling effort is adequate to establish an accurate measure of diet, or by demonstrating that the animals feed selectively from a broad range of prey options. In contrast, if the data suggest that a population has a broad dietary range, it is extremely unlikely that additional sampling or measuring food availability will suggest that the animal is in fact a dietary specialist; although additional sampling might of course further expand the documented dietary range.

We are confident that the sampling regime in our study has provided a reliable and unique representation of the prey composition (wet mass P:L from 1.5:1.0 to 21.4:1.0 and SEAc: 9.19) and realized nutritional niches (wet mass P:L from 1.5:1.0 to 15.2:1.0 and SEAc: 4.65) of gannets from the study population. Firstly, our data on prey and diet compositions over four seasons is consistent with a previous study of five years diet in gannets at Farewell Spit colony (Schuckard et al. 2012). Secondly, the range of macronutrients that we recorded in prey and diets consumed by gannets comprises most of the spectrum of marine fish wet mass concentrations of lipid (0.2% - 25.0%) and protein (17.0% - 25.0%) (Stansby 1969; Santhanam 2014), and it is thus unlikely that further sampling would have significantly expanded this. The data therefore strongly suggest that gannets are generalists at prey composition and macronutrient levels, similar to Argentine ants (*Linepithema humile*) and

wild boars (*Sus scrofa*) (Machovsky-Capuska *et al.* 2016a and Senior *et al.* 2016, respectively).

Variables that shape the nutritional niche

It has been suggested that a decrease in food sources will cause individuals to increase their time spent foraging and shift their diet pursuing different resources influencing niche width expansion in a population (Svanbäck & Bolnick 2007; Ceia *et al.* 2014). If only the amount of prey and their energy value are the main drivers of foraging (Stephens & Krebs 1986), we would expect to support this hypothesis showing that gannets increased their foraging effort and niche breadth (SEAc) under reduced prey availability. However, our MNNF showed that in 2011-2012 gannets had the widest prey composition niche and realized nutritional niche while spending the shortest amount of time foraging closer to the colony (MDC), whereas in 2015-2016 they exhibited their narrowest prey composition and realized nutritional niche breadths while spending more time searching for food (TFP), and foraging (h). A likely explanation could be that both patterns are subject to non-exclusive effects of prey availability and nutritional composition, although this remains to be established.

Variation in prey distribution, densities and quality at sea are driven by environmental factors, oceanographic processes and bathymetric features (Weimerskirch, Gault & Cherel 2005; Garthe *et al.* 2007). SST anomalies are known to drive spatial and temporal changes in the availability of pelagic prey (Montevecchi & Myers 1997; Perry *et al.* 2005). These movements are often linked to primary production events (Becker, Peery & Beissinger 2007) and also fish searching for suitable habitats while adjusting their thermal tolerance to survive (Bates *et al.* 2014). During warm water events (strong positive SSTa values), gannets increased their foraging habitat (UD95, km²), foraging trip duration (h) and total foraging path (km). This is consistent with previous suggestions that warm water events reduce

primary production and negatively influence prey availability (Becker, Peery & Beissinger 2007), imposing greater travel costs (time and distance) upon the forager and likely influencing their offspring (Fritz *et al.* 2003; Grémillet *et al.* 2004).

Although climate fluctuations are known to influence prey quality in marine (Wanless *et al.* 2005; Österblom *et al.* 2008) and terrestrial environments (Raubenheimer *et al.* 2015; Rothman *et al.* 2015), the mechanisms behind these effects are probably complex and remain unknown. In our study, strong warm water events negatively influenced the nutritional composition of prey species (wet mass proportions of P and L) and also diets consumed by gannets. The likely explanation is that the gannets' main prey are small anchovy, pilchard and garfish that feed mostly on plankton (Schuckard *et al.* 2012) and respond to regional plankton blooms under nutrient-rich conditions (Hunt *et al.* 1998; Paul, Taylor & Parkinson 2001). However, warmer waters are often more stratified and characterized by nutrient limitation and reduced plankton productivity (Richardson & Schoeman 2004; Behrenfeld *et al.* 2006). Thus, declines in nutrient availability strongly influence population structure, size, biomass and quality of prey species with subsequent implications on the trophic webs (Fuchs & Franks 2010).

Foraging animals, in the laboratory and the wild, link their movements to the distribution of their food sources (Masello *et al.* 2017). Understanding the factors that make a place a foraging 'hot-spot' is vital to unravel the drivers of prey preferences in marine predators. We presented unprecedented evidence in the form of nutriscaes, linking the nutritional composition with the geographic location of prey capture areas (UD50) of foraging gannets. Over the three seasons studied, the nutriscaes were patchily distributed, fluctuated from shallow to deeper areas and had different nutritional composition. Clearly, the temporal extent of this dataset and the proposed approach, brings a novel opportunity to better understand whether the prey consumed by wild predators could be supplementary

(similar P:L ratios across prey) or complementary (different P:L ratios) with respect to the diet. Thus this approach could become the stepping stone for research of foraging strategies in marine predators by investigating habitat use and food patch selection and depletion in relation to prey and diet composition and nutrition as previously seen in Guerezas (*Colobus guereza*) (Johnson *et al.* 2017).

Bearing in mind that prey and geographic location was obtained from foraging gannets arriving to colony, nutriscapes should not be considered as a surrogate for qualitative or quantitative prey availability. From our point of view, in spite of the small sample size presented herein, this novel approach provides a unique opportunity to reconstruct foraging behaviors and habitat use linked with geographic location, abiotic factors (e.g. salinity, chlorophyll, sea surface temperature, bathymetry and others) and temporal measures of resource acquisition quantified as specific nutrients. The use of bio-logging sensors including Animal-borne Video and Environmental data collection systems (AEVDs) combined with NG has been proven to yield new insights into marine wild predators nutritional ecology (Machovsky-Capuska *et al.* 2016c) and could be vital to enhance the resolution and the expansion on the use of nutriscapes. This cutting-edge approach could contribute to either marine, freshwater or terrestrial environments, playing a fundamental role in assessing nutritional decisions based on the nutritional composition of a wide range of species in the wild. Nutriscapes can provide fresh insights in a wide range of research fields including: i) predicting the distribution and expansion of invasive species; ii) understanding the dietary needs and the nutritional composition and availability of habitats for endangered species; iii) exploring critical habitats for species translocations; iv) understanding the location and nutritional value of geographic areas prone to human-wildlife conflict (e.g. fisheries); and v) unravelling traveling routes for migratory species based on nutrient composition and availability.

Dietary generalism has been suggested to evolve in heterogeneous environments, whereas specialism is a response to a homogeneous environment (Senior *et al.* 2015). Overall, our study suggests that gannets: i) display a high degree of prey and diet composition generalism, being able to prey upon species that vary in nutritional composition, and have a wide nutritional range in their diets; ii) across seasons, nutritional landscapes varied in prey composition, over space, time and bathymetry and iii) during warm water events (strong positive SSTa), gannets expanded their foraging habitat, increased their foraging trip duration while consuming prey and diets low in nutritional composition. Our results highlight the importance of quantifying and characterizing the prey composition and realized nutritional niches to test broader ecological questions to better understand the extent of dietary generalism in the wild.

Data Accessibility

Data used in this manuscript are available from Pangea ® Data Repository: <https://doi.pangaea.de/10.1594/PANGAEA.890146> (Machovsky-Capuska et al 2018).

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Table 1. Diet composition of adult-chick rearing Australasian gannets estimated from 172 dietary samples collected over four different breeding seasons at Farewell Spit colony (New Zealand). The sample size is given after each season in brackets. M% = wet mass, N% = numerical abundance, F%=frequency of occurrence.

Species	Season 2011-2012 (n=24)			Season 2013-2014 (n=35)			Season 2014-2015 (n=50)			Season 2015-2016 (n=63)		
	M %	N%	F%	M %	N%	F%	M %	N%	F%	M %	N%	F%
Pilchard	53.57	86.15	66.67	22.56	8.53	20.00	–	–	–	35.09	10.40	29.69
Anchovy	0.57	3.08	8.33	1.89	1.71	5.71	22.89	43.94	42.00	40.67	71.71	67.19
Squid	12.36	3.85	16.67	0.70	3.41	5.71	8.45	4.04	10.00	6.27	1.94	10.94
Garfish	0.37	1.54	4.17	48.24	83.96	60.00	46.40	37.37	46.00	5.90	4.99	4.69
Yellow Tail Jack Mackerel	19.97	3.08	12.50	21.94	1.71	14.29	10.48	1.52	6.00	–	–	–
Kahawai	6.23	1.54	8.33	3.65	0.34	2.86	–	–	–	–	–	–
Barracouta	6.93	0.77	4.17	–	–	–	–	–	–	–	–	–
Yellow Eye mullet	–	–	–	1.02	0.34	2.86	11.77	13.13	10.00	–	–	–
Saury	–	–	–	–	–	–	–	–	–	12.07	10.96	9.38

Table 2. Foraging habitat and trip characteristics of adult-chick rearing Australasian gannets at Farewell Spit colony over three different breeding seasons. Data presented as mean \pm standard error (SE).

Parameter	2011-2012	2014-2015	2015-2016
<i>Foraging habitat</i>			
Sample size (N)	11	17	11
UD95 Individuals (km ²)	1100.89 \pm 247.06	1367.41 \pm 432.46	1374.24 \pm 473.39
UD50 Individuals (km ²)	222.54 \pm 83.36	238.99 \pm 65.48	273.05 \pm 131.00
Bathymetry (m)	44.86 \pm 65.15	74.78 \pm 28.84	90.65 \pm 25.94
<i>Foraging trip characteristics</i>			
Max. distance to colony (km)	44.93 \pm 9.27	60.52 \pm 7.48	57.24 \pm 5.79
Total foraging path (km)	227.91 \pm 64.72	262.64 \pm 35.21	289.55 \pm 27.55
Foraging trip duration (h)	14.71 \pm 3.71	14.88 \pm 2.34	26.36 \pm 2.97
Transiting time (h)	2.27 \pm 1.75	1.82 \pm 1.94	3.34 \pm 2.82
Foraging time (h)	2.97 \pm 2.45	3.09 \pm 3.45	4.21 \pm 3.48
Total dive duration (s)	6.26 \pm 0.87	3.66 \pm 0.46	5.25 \pm 0.63

Table 3. Linear Models (LM) testing the interactions between Sea Surface Temperature Anomaly (SSTa) on foraging habitat and foraging behaviour. SSTa-: colder water periods and SSTa+: warmer water periods. Data presented as mean \pm standard error (SE). Significant differences marked in bold.

Parameter	SSTa-	SSTa+	LM	P
<i>Foraging habitat</i>				
UD95 Individuals (km ²)	1110.89 \pm 100.86	1367.41 \pm 101.93	<i>F</i> =3.72	<0.05
UD50 Individuals (km ²)	222.53 \pm 34.03	241.48 \pm 17.89	<i>F</i> =0.71	0.40
Bathymetry (m)	52.23 \pm 17.31	88.72 \pm 3.29	<i>F</i> =4.64	<0.01
<i>Foraging trip characteristics</i>				
Max. distance to colony (km)	58.26 \pm 8.32	74.91 \pm 5.52	<i>F</i> =6.71	<0.01
Total foraging path (km)	251.41 \pm 22.98	295.09 \pm 22.47	<i>F</i> =4.38	<0.01
Foraging trip duration (h)	13.51 \pm 3.46	21.34 \pm 1.79	<i>F</i> =5.74	<0.01
Transiting time (h)	2.59 \pm 0.67	4.09 \pm 0.40	<i>F</i> =5.26	<0.01
Foraging time (h)	3.37 \pm 0.96	5.71 \pm 0.62	<i>F</i> =5.61	<0.01
Total dive duration (s)	4.75 \pm 0.49	2.67 \pm 0.07	<i>F</i> =55.34	<0.0001

Table 4. Linear Models (LM) testing the interactions between Sea Surface Temperature Anomaly (SSTa) on the nutritional composition of prey and diets (wet mass proportions of P, L, W and LnPL) of adult chick rearing Australasian gannets. SSTa-: colder water periods and SSTa+: warmer water periods. Data presented as mean \pm standard error (SE). Significant differences marked in bold.

<u>Parameter</u>	<u>SSTa-</u>	<u>SSTa+</u>	<u>LM</u>	<u>P</u>
<i>Prey</i>				
Protein	20.88 \pm 0.25	19.79 \pm 0.32	<i>F</i> =15.66	<0.001
Lipid	2.68 \pm 0.29	2.03 \pm 0.16	<i>F</i> =4.39	<0.01
Water	72.16 \pm 0.42	73.68 \pm 0.37	<i>F</i> =3.12	<0.05
LnPL	2.22 \pm 0.13	2.47 \pm 0.16	<i>F</i> =8.82	<0.001
<i>Diet</i>				
Protein	21.71 \pm 0.17	20.06 \pm 0.13	<i>F</i> =3.62	<0.01
Lipid	2.89 \pm 0.21	2.25 \pm 0.06	<i>F</i> =20.30	<0.0001
Water	73.64 \pm 0.30	75.70 \pm 0.11	<i>F</i> =0.34	0.56
LnPL	2.11 \pm 0.07	2.36 \pm 0.11	<i>F</i> =20.20	<0.0001

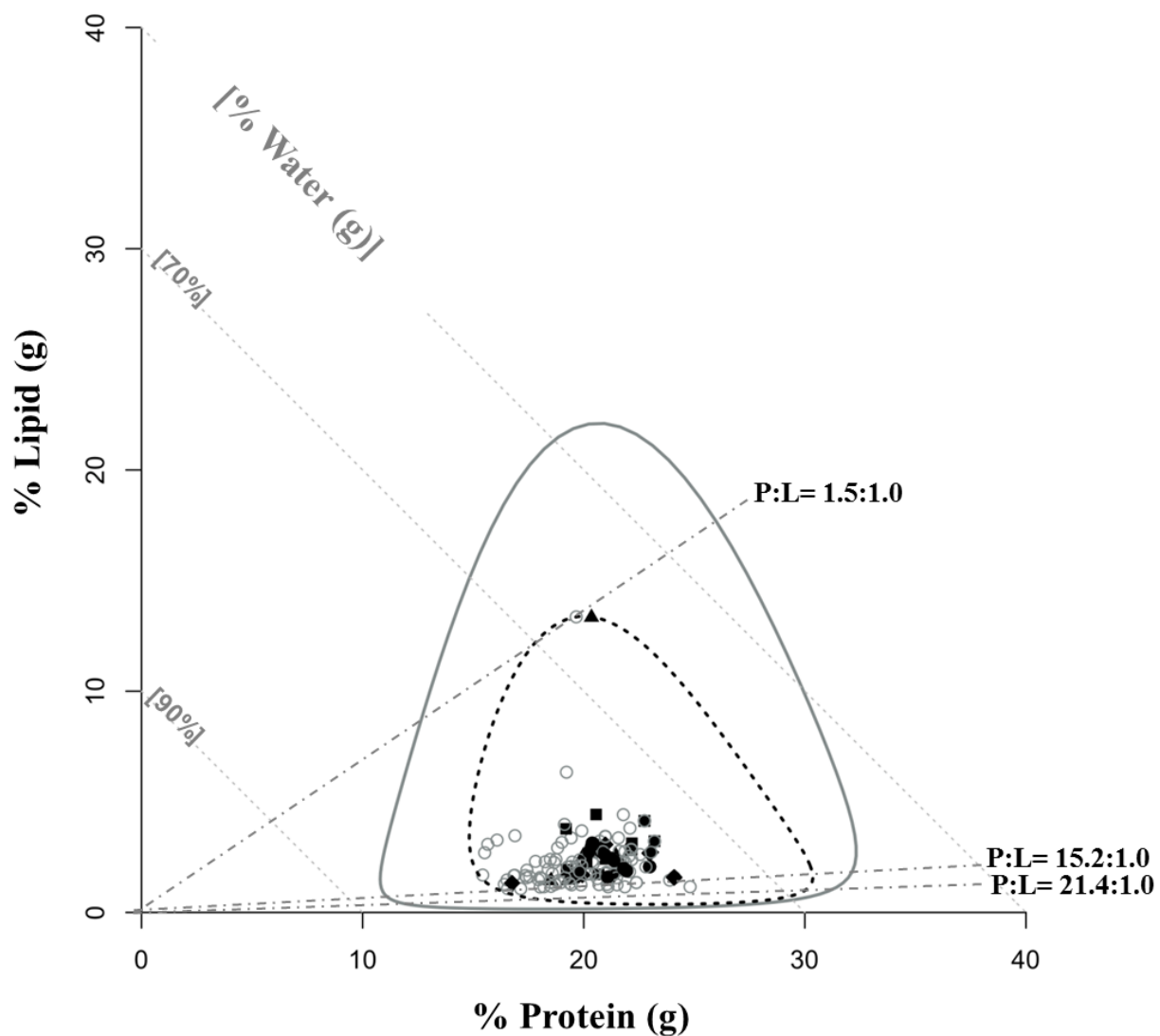


Figure 1. Right-angled mixture triangle (RMT) showing foraging choices of chick-rearing adult Australasian gannets at Farewell Spit colony. Nutritional composition of prey (grey hollow circles) and diets (black solid symbols). Each prey and diet represents a proportional mixture of protein (P), lipid (L) and water (W). To geometrically define prey and diets in an RMT, % P is plotted against % L. Considering that the 3 components in the mixture sum to 100%, plotting % P (first axis) and % L (second axis) will automatically reflect the value of % W in the third axis (Raubenheimer 2011). The prey composition niche (all the prey consumed by gannets, Machovsky-Capuska *et al.* 2016) breadth is measured as the area of standard ellipse (SEAc: 9.19, grey solid ellipse). The realized nutritional niche breadth of gannets (all individual diets from the four breeding seasons studied (2011-2012: triangle, 2013-2014: square, 2014-2015: diamond and 2015-2016: circle) is measured as the area of standard ellipse (SEAc: 4.65, black dotted ellipse).

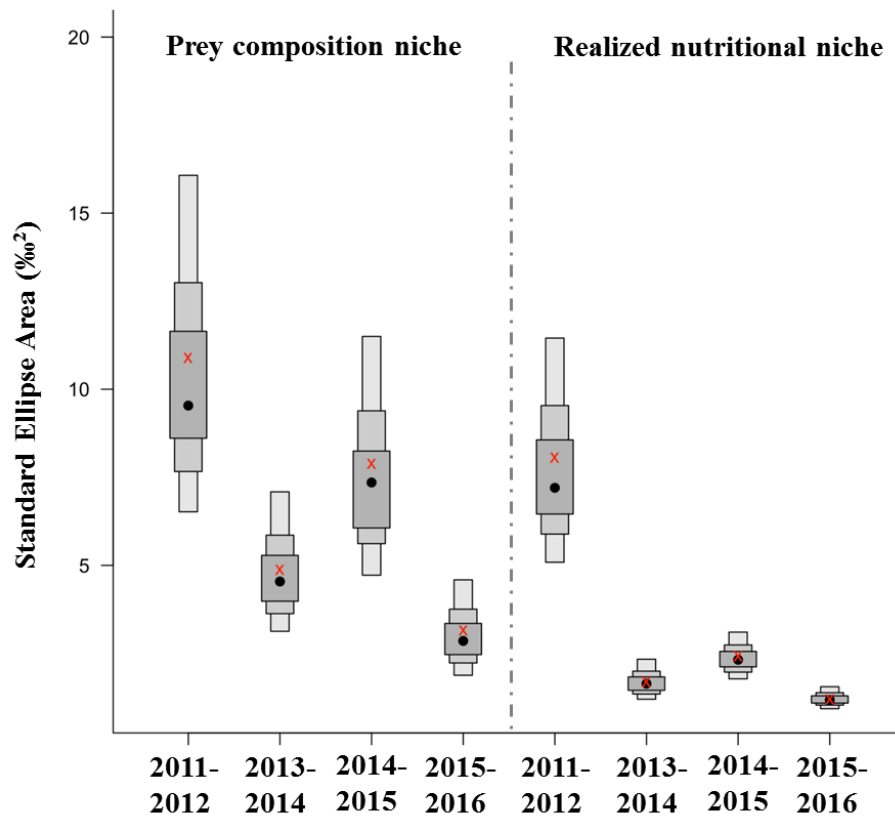


Figure 2. Inter-annual differences in the nutritional niche breadth of Australasian gannets. The boxplot shows the credible interval (CI) range for the estimated ellipse area (SEAb) for prey composition niches and realized nutritional niches (diets) across seasons. Boxed areas represent the 50, 75 and 95% credible intervals for the estimated ellipse areas. Black dots and the red crosses represent the mode of SEAb and the maximum likelihood estimates SEAc, respectively. All boxed areas denote significant difference ($P < 0.0001$).

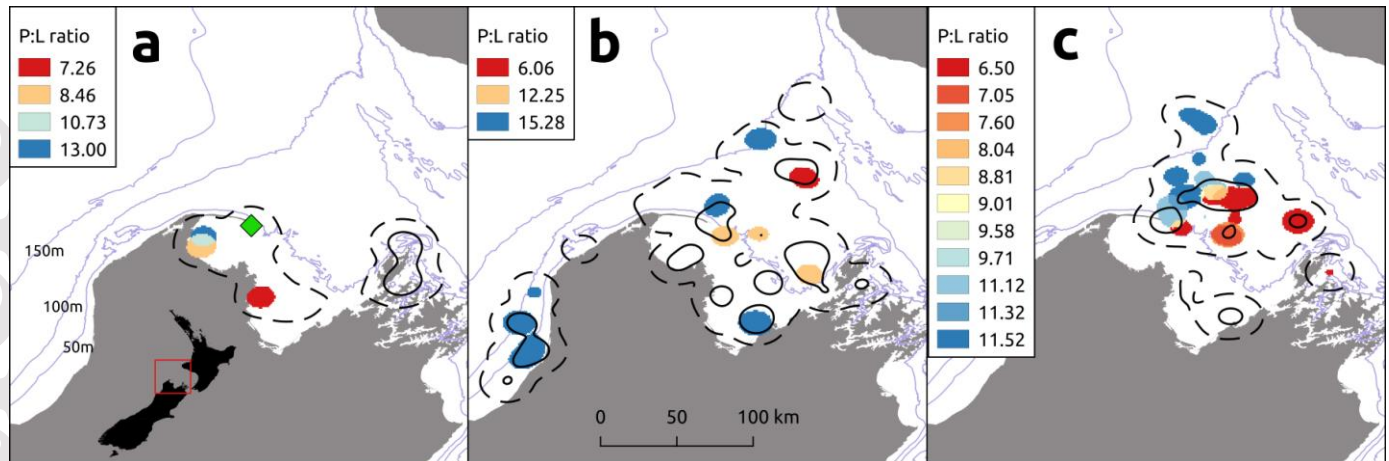


Figure 3. Foraging habitat and dive locations of adult chick-rearing Australasian gannets from Farewell Spit colony (New Zealand, green diamond) during three chick-rearing seasons: **a)** 2011-2012, **b)** 2014-2015 and **c)** 2015-2016. Kernel density Utilization Distributions (UD) show habitat used (UD 95: dotted lines) and prey capture areas (UD 50: solid lines). Nutriscape maps linking nutritional content of prey (wet mass protein-to-lipid ratios -P:L-) to the most likely geographic area of captured (coloured areas) and bathymetry. Isobaths expressed in meters (m).