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ORIGINAL PAPER

Sex-specific macronutrient foraging strategies in a highly successful marine predator: the Australasian gannet

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Abstract The foraging challenge for predators is to find and capture food with adequate levels of energy and nutrients. Marine predators require particularly sophisticated foraging strategies that enable them to balance self- and offspring-feeding, and also in many circumstances simultaneously consider the nutritional constraints of their partners. Here we combined the use of dietary analysis, proximate composition and nutritional geometry (right-angled mixture triangle nutritional models) to examine the macronutrient preferences of Australasian gannets (*Morus serrator*) at Farewell Spit gannetry in New Zealand. Our results showed intra- and inter-specific variation in the protein, lipid and water composition of prey captured by our sample of 111 Australasian gannets. In addition, we observed significant differences in the Australasian gannets' nutritional niche between seasons. We provide evidence of sex-specific macronutrient foraging strategies in a successful marine predator in the wild. We have shown that in spite of fluctuations in the nutritional composition of foods available to Australasian gannets, males consistently capture prey with higher protein-to-lipid ratios and lower lipid-to-water ratios than females. These results aid to better understand the evolutionary relationship between macronutrient selection and sex-specific traits in wild animals. They also suggest an incentive for these predators to combine individually imbalanced but nutritionally complementary foods to achieve dietary balance, further highlighting the likelihood that prey selection is guided by the balance of macronutrients, rather than energy alone.

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Introduction

For predators, the capture of a combination of foods that contains the required levels of energy and nutrients is an important challenge (Simpson and Raubenheimer 2012). Recent studies on a wide range of animals suggests that foraging is targeted to the specific amount and balance of nutrients ingested, rather than the gain of any specific nutritional currency such as energy (Raubenheimer and Simpson 1997).

In order to meet their nutritional goals, marine predators must deal with multiple challenges across different scales. First, foods are complex mixtures of many nutrients parcelled at differing ratios, and each nutrient has its

own functional implications for the forager (Simpson and Raubenheimer 2012). In addition, the nutritional composition of foods varies geographically (Tait et al. 2014; Rothman et al. 2015). Second, within populations optimal nutrient intake can be variable, for example where nutrient requirements are sex- or age specific (Raubenheimer et al. 2009; Senior et al. 2015). Third, in order to balance nutrient intake in a fluctuating environment, foragers must continuously adjust their foraging behaviour to meet their own (potentially changing) nutritional requirements.

Understanding the nutrient requirements and foraging goals of animals is important to predict how animals will respond to environmental changes in prey availability (Raubenheimer et al. 2012; Machovsky-Capuska et al. 2016). The challenges faced by foragers in marine environments are particularity complex. Within these habitats, foods may be especially sparse and patchily distributed and are subject to oceanic and climatic fluctuations, as well as additional human pressures (Norman 2000; Hobday et al. 2013; Srinivasan et al. 2015). Drastic shifts in climate-related regimes are believed to be responsible for the decrease in availability of high-quality prey species (in terms of energy and lipid contents) and an increase in low-quality foods, which has negatively influenced marine predator populations around the world (Österblom et al. 2008). Operating in such a complex environment, marine predators require particularly sophisticated foraging strategies that enable them to balance self- and offspring-feeding, and also in many circumstances simultaneously consider the nutritional constraints of their partners (Weimerskirch et al. 1994; Machovsky-Capuska et al. 2014a; Malinowski and Herzing 2015). Seabird chicks are under constant age-related fluctuations in lipid, protein, water and energy density until they reach functional maturity and are able to feed for themselves (Navarro 1992). To successfully rear offspring, a wide range of seabirds have biparental care, where the parents divide the costs of reproduction and foraging by pooling resources and effort (Lack 1968; Hamer et al. 2006; Quillfeldt et al. 2006). The roles adopted by parents in these divisions of labour could be influenced by sex differences in body morphology, also known as 'sexual dimorphism' (Wright and Cuthill 1989; Mock and Fujioka 1990). Dimorphic body sizes are known to influence foraging strategies in seabirds and could lead to differences in diving behaviour (Zavalaga et al. 2007), prey consumption (Bearhop et al. 2006), time spent foraging (Welcker et al. 2009; Pinet et al. 2012), foraging effort (Gray and Hamer 2001; Peck and Congdon 2006; Thaxter et al. 2009) and overall foraging efficiency (Weimerskirch et al. 1997; González-Solís et al. 2000; Shaffer et al. 2001).

Although it was initially thought that all sex-specific foraging strategies were driven largely by size differences, extensive evidence suggests that sex-specific differences in foraging behaviour also exist within monomorphic seabird species (see Elliott et al. 2010; Hedd et al. 2014). Gannets (*Morus* spp.), in particular, have been extensively studied, shedding light on sex-specific foraging behaviour. These long-lived marine predators with biparental care have been conventionally considered monomorphic species, but a recent study suggest morphometric differences between sexes in two Australian colonies (Angel et al. 2015). In Northern gannets (*M. bassanus*), sex-specific differences have been observed in habitat use (Lewis et al. 2004; Cleasby et al. 2015), diving behaviour (Lewis et al. 2002) and prey consumption (Stauss et al. 2012). In Cape gannets (*M. capensis*), asymmetries between the sexes have been noted in reproductive investment (Bijleveld and Mullers 2009), foraging distance and foraging duration (Mullers and Navarro 2010). Finally, in Australasian gannets (*M. serrator*) evidence for sexual differences in nest attendance, diving behaviour and stable isotope signatures (Ismar 2010) and recently body size (Angel et al. 2015) have been observed. It has been suggested that sexual differences in the foraging behaviours are likely to be associated with competition or aggression during nest selection (Barbraud 2000; Paiva et al. 2013) or different nutritional requirements of males and females (Lewis et al. 2002), although this remains to be established.

Understanding the relationships between nutrition, behaviour, ecology, morphology and physiology is a central aim in nutritional ecology (Raubenheimer et al. 2009, 2015). Gannets are carnivorous central place foragers (Machovsky-Capuska et al. 2012, 2014a), and a developing model species for testing field-based nutritional ecology questions (Tait et al. 2014). Here we combined the use of dietary analysis, proximate composition and nutritional geometry (right-angled mixture triangle nutritional models—RMT) to examine the macronutrient preferences of Australasian gannets at Farewell Spit gannetry (FS) in New Zealand. We addressed three questions to provide a better understanding of the nature of macronutrient (protein, lipid) and water, sex-specific foraging strategies in marine predators: (a) Does the macronutrient (protein, lipid) and water composition vary between prey species and temporally? (b) Do female and male Australasian gannets target specific prey? (c) Does the nutritional niche in which Australasian gannets forage vary between sexes and temporally? Given that Australasian gannets show sex-specific foraging strategies, we predict that males and females should consume different prey that varies intra- and interspecifically in their macronutrient composition. In addition, Australasian gannets should exhibit inter-annual variation in their diet and nutritional niche which are likely to represent fluctuations in the availability of prey (Machovsky-Capuska et al. 2016).

Materials and methods

Study area

The study was conducted during the chick-rearing period in December and January 2011–2012, 2013–2014 and 2014–2015 at FS, which is located at the northern end of the South Island, New Zealand (40°33′S, 173°01′E). The FS gannetry in Golden Bay was established in 1983, and since then, the population has increased by an average of 11.5 % per annum, to around 3900 pairs in 2011 (Schuckard et al. 2012).

Capture and handling of birds

Adult Australasian gannets rearing 2- to 5-week-old chicks were captured with a blunt-tip shepherd's crook from nests located on the periphery of the colony. A total of 111 regurgitations were collected over the three seasons studied [2011–2012, females ($n = 12$) and males ($n = 12$); 2013–2014, females ($n = 18$) and males ($n = 18$); and 2014–2015, females ($n = 25$) and males ($n = 26$)]. In addition, captured foods transported in the proventriculus are highly likely to be kept undigested (Machovsky-Capuska et al. 2011a), and are exposed to minimal macronutrient and water fluctuations (Montevecchi and Piatt 1987). For this reason, the birds used in the present study were captured immediately after they arrived at the colony, before they fed their chicks. Captured Australasian gannets were banded with individually numbered metal rings on their leg and secondary covert feathers were collected for DNA sex identification following Fridolfsson and Ellegren (1999). Samples were collected in separate polythene bags from adult Australasian gannets on active nests that voluntarily regurgitated during handling. Following Machovsky-Capuska et al. (2014a), to avoid unnecessary recapture birds that regurgitated were marked blue on the chest and those that did not were marked black using Sharpie markers©. Capture took <10 min, and birds were 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).

Prey composition of diet

Regurgitated samples were defrosted and weighed (to within 0.1 g) before being separated by taxa. Digestion codes were assigned to retrieved prey items (following Meynier et al. 2008), and prey species were identified to the lowest possible taxonomic level using published guides (Paulin et al. 1989). Individual prey items were counted, identified and individually weighed (to within 0.1 g when possible), and fork lengths (FL) of fish and mantle lengths of cephalopods were measured (to within 0.1 mm) using callipers. Weight of the regurgitation was calculated as the sum of the individual prey items' mass, and each prey species was assigned a mass percentage (M %), calculated as the percentage contribution of each prey species to the total weight of the regurgitation following Duffy and Jackson (1986). In addition, a numerical abundance percentage (N %) was calculated as the percentage of the total number of prey items contributed by individuals of a particular species, and a frequency of occurrence percentage (F %) calculated as the percentage of birds that had a particular species in their diet (Schuckard et al. 2012).

Macronutrient composition of prey

Following Tait et al. (2014), undigested samples of the main prey species found in the diets of Australasian gannets were selected for proximate composition analyses. Prior to analysis, each sample was partially thawed and weighed to within 0.1 g, dried overnight in a convection oven at 60 °C and ground to powder with a laboratory mill. We used Kjeldahl assay or combustion analysis to measure nitrogen, which was then converted to protein by multiplying by a factor of 6.25 (AOAC 981.10; see AOAC 2005 for more details). We used Mojonnier method that combines a mixture of ethyl ether and petroleum ether to measure total lipid content (AOAC 954.02). Moisture (hereafter water) was measured by drying the sample in a convection oven at 125 °C (AOAC 950.46; AOAC 2002) and combining water loss with initial loss from the overnight dry down. Ash was measured by ignition in a furnace at 550 °C (AOAC 920.153; AOAC 2005). Following Raubenheimer and Rothman (2013), macronutrient masses were converted to energy using conversion factors (protein = 17 kJ/g and lipid = 37 kJ/g).

Statistical analysis

All analyses were performed in statistical programming environment R V.3.2.1 (R Core Team 2015). Linear and generalized linear models (LMs and GLMs) were implemented using the 'lm' and 'glm' functions in the *base* package (unless otherwise stated), and linear mixed models (LMMs) were implemented in the *lme4* package (Bates et al. 2015).

Question 1: Does the macronutrient (protein, lipid) and water composition vary between prey species and temporally?

To evaluate the between-species variation in the proximate composition of prey fish two LMMs were implemented. Each LMM was fitted against the intercept, with a random effect for the species ID in order to estimate between-species variance. The first LMM fitted the ratio of energy-yielding nutrients within a prey by fitting the log ratio of the proportion of protein to lipid (lnPL) from each prey as the response. The second LMM fitted the log ratio of energy-yielding components to water (lnEW) from each prey as the response. The statistical significance of estimates of between-species variance was assessed using likelihood ratio tests, implemented using the 'rand' function in the package *lmerTest* (Kuznetsova et al. 2015). Random effects (as opposed to fixed effects) were used to estimate between-species variance, due to the large number of species in the dataset and the fact that we have variable sample sizes for each species. In addition, we note that random-effects estimates of variance may be considered more conservative than fixed effects. We also explored how the composition of prey species (lnPL and lnEW) changed from season to season. A separate LM was fitted for each response, with the compositional ratio of interest from each sample of a fish as the response, and a categorical predictor for the year in which the fish was sampled as the predictor.

Question 2: Do female and male Australasian gannets target different prey combinations?

To assess differences between the regurgitated prey of males and females, we explored models fitting the effect of sex (female or male) as a categorical fixed effect, but also evaluated the effects of sampling season (again categorical; 2012, 2014 or 2015), using additive and interactive models. In all cases, we report results from the model with the lowest Akaike Information Criterion corrected (AICc) for small sample size (given that the AICc converge to the AIC when analysing with large sample sizes, it has been suggested that the former should be used as a default; Symonds and Moussalli 2011). Differences in the number of fish regurgitated by females and males were compared using a poisson-family GLM, where the response was the number of fish in regurgitation. Differences in the average mass of an individual prey item between males and females were assessed with a LMM, where the response was the mass of each regurgitated prey item. Because the prey was the unit of analysis, we included a random factor giving the identity of the bird that regurgitated the prey (several prey may come from the same bird). Total mass of regurgitation was analysed as a response in a LM. Differences in prey species composition between males and females were explored using a multinomial GLM, implemented using the 'multinom' function in the *nnet* package (Venables and Ripley 2002), where the response was the counts of each prey species regurgitated by an individual, predicted by the sex of the bird. Statistical significance of multinomial GLM estimates was inferred when the 95 % confidence interval (CI) for the estimate did not span zero.

For those prey species previously recorded in the diets of Australasian gannets (as mentioned above), we obtained stable isotope signatures from the same geographic area from Handley et al. (2011). Following Chiaradia et al. (2010) and Madigan et al. (2012), prey were grouped into three different trophic-level categories in relation to $\delta^{15}N$ values and classified as (a) high [kahawai (*Arripis trutta*) and garfish (*Hyporhamphus ihi*) > 13.00 ‰], (b) medium [yellow eye mullet (*Aldrichetta forsteri*), arrow squid (*Nototodarus* spp.) and yellow tail jack mackerel (*Trachurus* spp.), >12.00 and <13.00 ‰] and (c) low [pilchard (*Sardinops neopilchardus*) and anchovy (*Engraulis australis*), <12.00 ‰]. We assessed whether the contribution of species from differing trophic levels to regurgitation differed between males and females, using multivariate LMs (following Kronmal 1993). For each bird, we calculated the total weight of fish regurgitated from each trophic level (one, two, or three), and fitted a separate LM for each (i.e. three models). In each model, the response was the number of grams of fish from a given trophic level regurgitated by the bird, predicted by the sex of the bird. Given that larger regurgitations have a higher mass, we corrected for total mass of the regurgitation statistically (*Z*-transformed, and fitted with interaction against bird sex). Whilst the most intuitive interpretation of these data may be as a proportion (or %) of total weight of the regurgitation by each individual, the recommended logit transformation (Warton and Hui 2010) for proportions failed in our dataset as it simultaneously contains values of both 0 and 1.

Question 3: Does the nutritional niche in which Australasian gannets forage vary between sexes and temporally?

For each prey species, in each year, we first calculated the mean composition in terms of protein, lipid and water; logit transformation was deemed the most appropriate method to normalize proportions. Using the year-specific mean prey nutrient compositions, we then estimated the proportion of protein, lipid and water in each regurgitation based on the contribution of each prey species (proportionally by mass) to the regurgitation. We then calculated lnPL and lnEW (as above), the log ratio of lipid to water (lnLW), as well as an estimate of the total grams of protein, lipid and water within each regurgitation (i.e. total weight multiplied by the

Table 1 Random-effects estimates from linear mixed models of the between-species and residual variance (and as standard deviation; SD) in the log ratio of protein to lipid composition (lnPL) and log energy-yield to water components (lnEW) of prey species

Response	Effect	Variance	SD	χ^2	p
lnPL	Species	0.619	0.787	15.10	<0.001
	Residual	0.152	0.389		
lnEW	Species	0.029	0.170	27.9	<0.001
	Residual	0.015	0.123		

χ^2 and p values were obtained by likelihood ratio test (degrees of freedom = 1)

proportion of the component therein). Differences between males and females in these responses were then analysed in separate LMMs. As above, we explored interactions between sex and year as fixed effects with AICc, along with a random effect controlling for the date on which the sample was taken.

The macronutrient composition (expressed as % of wet mass) of prey species and diets of Australasian gannets during three different breeding seasons were plotted using RMT models (Raubenheimer 2011). To display the proportional composition of prey and diets in an RMT, each of the three model components—here protein (P), lipid (L) and water (W)—is expressed as a mass percentage of the sum of the three: for example, $P = P/(P + L + W) \times 100$. Because the three components sum to 100 %, if any two are plotted against each other (e.g. % P on the x-axis vs. % L on the y-axis), the value third (W %) is implicit in the position of each point, with W % decreasing with distance from the origin.

Results

Question 1: Does the macronutrient (protein, lipid) and water composition vary between prey species and temporally?

Across all prey species, the composition of energy-yielding nutrients was significantly skewed towards protein, rather than lipid (lnPL est. ± SE = 1.90 ± 0.29, $df = 5.17$, $t = 6.66$, $p < 0.05$, LMM; see Supplementary information Table S1), and the mean LMM estimate back-transformed (exponential) to a ratio was 6.71 parts protein to 1.00 part lipid. However, the ratio of these two nutrients varied significantly between prey species (Table 1). The estimates of ratio of energy-yield to water in prey species show that on average prey species are largely comprised of water (lnEW est. ± SE = −1.14 ± 0.06, $df = 4.96$, $t = -17.96$, $p < 0.001$, LMM; see Supplementary information Table S2), and on average this ratio is 0.32 parts energy-yielding macronutrient to 1.00 part water. Again this ratio varied significantly between species (Table 1).

The mean composition of a number of species also differed between sampling years. Garfish, for example, showed a significantly higher ratio of protein to lipid in the 2015 season than the 2014 season (lnPL est.$_{\text{Year.2015}}$ ± SE = 0.68 ± 0.14, $df = 10$, $t = 4.99$, $p < 0.001$, LM; see Supplementary information Table S3 for all species), although no substantial or significant difference in the ratio of energy to water (lnEW est.$_{\text{Year.2015}}$ ± SE = 0.03 ± 0.05, $df = 10$, $t = 0.62$, $p = 0.55$, LM). Pilchards also showed between-season differences in their composition, with a decline in the ratio of protein to lipid (lnPL est.$_{\text{Year.2014}}$ ± SE = −0.43 ± 0.14, $df = 6$, $t = -3.03$, $p < 0.05$, LM), and an increase in the ratio of energy to water being observed between 2012 and 2014 (lnEW est.$_{\text{Year.2014}}$ ± SE = 0.15 ± 0.03, $df = 6$, $t = 5.15$, $p < 0.01$, LM). Other species were more stable across seasons. Squid for example showed no significant differences in the ratio of protein to lipid components, the ratio of energy to water.

The RMT models show the differences in the mass contribution (mass %, wet weight) of each prey towards the diet on each of the breeding seasons studied (Fig. 1a–c). During the 2011–2012 breeding season, *M. serrator* consumed seven different prey species that varied in their protein-to-lipid ratios (P:L) from 1.5:1.0 (barracouta) to 13.3:1.0 (yellow-tailed jack mackerel; Fig. 1a). In the following season (2013–2014), they consumed six different prey species with a wide range of P:L ratios that varied from 5.5:1.0 (anchovy) to 12.7:1.0 (yellow eye mullet) (Fig. 1b). Finally, in the 2014–2015 season, *M. serrator* only preyed upon five species and their P:L ratios varied from 6.1:1.0 (yellow eye mullet) to 15.5:1.0 (garfish) (Fig. 1b).

The P:L ratios of the diets varied considerably over the different seasons studied (2011–2012: 8.4:1.0; 2013–2014: 7.6:1.0; 2014–2015: 12.8:1.0, Fig. 1d). Although *M. serrator* relied on three prey species that jointly contributed 80 % of wet mass of the diets, they consumed different combinations of prey over the breeding seasons studied to achieve their nutrient gains (Fig. 1a–c).

Question 2: Do female and male Australasian gannets target specific prey?

For differences in the number of prey items, a GLM including sex, season and their interaction was favoured by AICc. The number of fish in female regurgitations was lower in 2014 and 2015 than 2012 (Fig. 2a), and the difference for 2015 was statistically significant (est.$_{\text{Year.2015}}$ ± SE = −0.35 ± 0.15, $df = 105$, $z = -2.398$, $p < 0.05$, GLM; see Supplementary information Table S4 for full GLM output). In 2012, the mean number of prey regurgitated by males

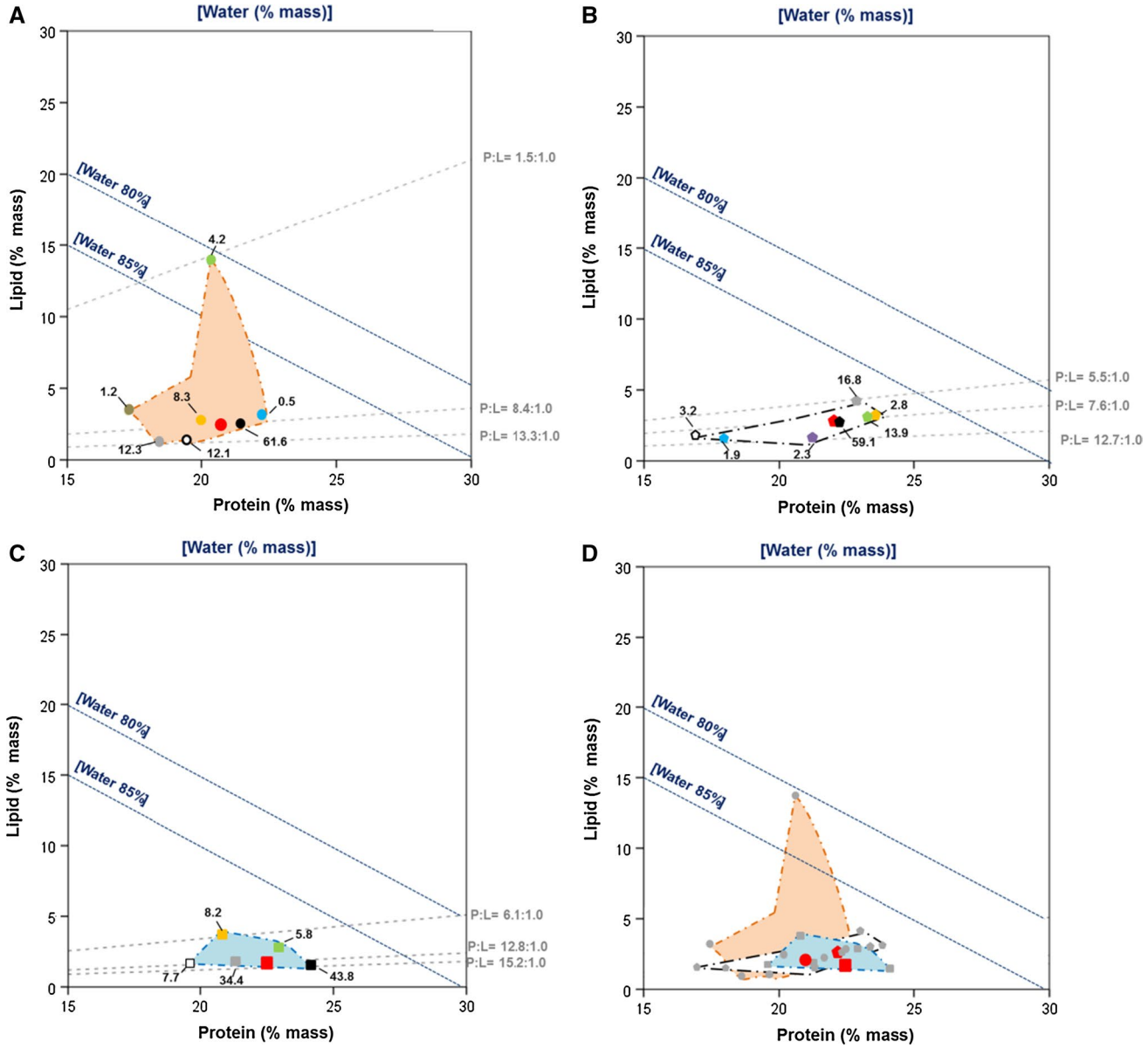

Fig. 1 Right-angled mixture triangle (RMT) showing the foods and diet macronutrient composition and the nutrient spaces of chick-rearing adult Australasian gannets. **a** Contribution in mass (M %, wet weight) of each foods (*black* = pilchard; *grey* = squid; *light green* = barracouta; *gold* = kahawai; *hollow* = yellow tail jack mackerel; *light blue* = garfish and *light brown* = anchovy) towards the diet (*red*) during 2011–2012 breeding season. **b** Contribution in mass (M %, wet weight) of each foods (*black* = garfish; *grey* = pilchard; *light green* = yellow tail jack mackerel; *gold* = kahawai; *hollow* = anchovy and *light blue* = squid) towards the diet (*red*) during 2013–2014 breeding season. **c** Contribution in mass (M %, wet weight) of each foods (*black* = garfish; *grey* = anchovy; *light green* = yellow tail jack mackerel; *gold* = yellow eye mullet and *hollow* = squid) towards the diet (*red*) during 2014–2015 breeding season. **d** A comparison of the different nutrient niches from the three different breeding seasons studied. *Pink area* and *circles* = 2011–2012; *black area* and *polygons* = 2013–2014 and *blue area* and *boxes* = 2014–2015. *Grey* = prey species and *red* = diet

was lower than females (est.$_{Sex}$ ± SE = −0.66 ± 0.20, $df = 105$, $z = -3.408$, $p < 0.001$, GLM; Fig. 2a). However, in 2014, an opposing sex-specific pattern was observed and we detected a statistically significant interaction between the number of prey items regurgitated in 2012–2014 and sex of the bird (number of fish est.$_{Year.2014:Sex.M}$ ± SE = 1.12 ± 0.23, $df = 105$, $z = 4.82$, $p < 0.001$, GLM; Fig. 2a). For mean mass of fish, again AICc was lowest for the model containing an interaction between sex and year. The mean mass of a prey item regurgitated by males and females showed the opposite pattern to the number of prey regurgitated. In 2012 and 2015, males regurgitated heavier prey than females on average, although this difference was non-significant (Fig. 2b; see Supplementary information Table

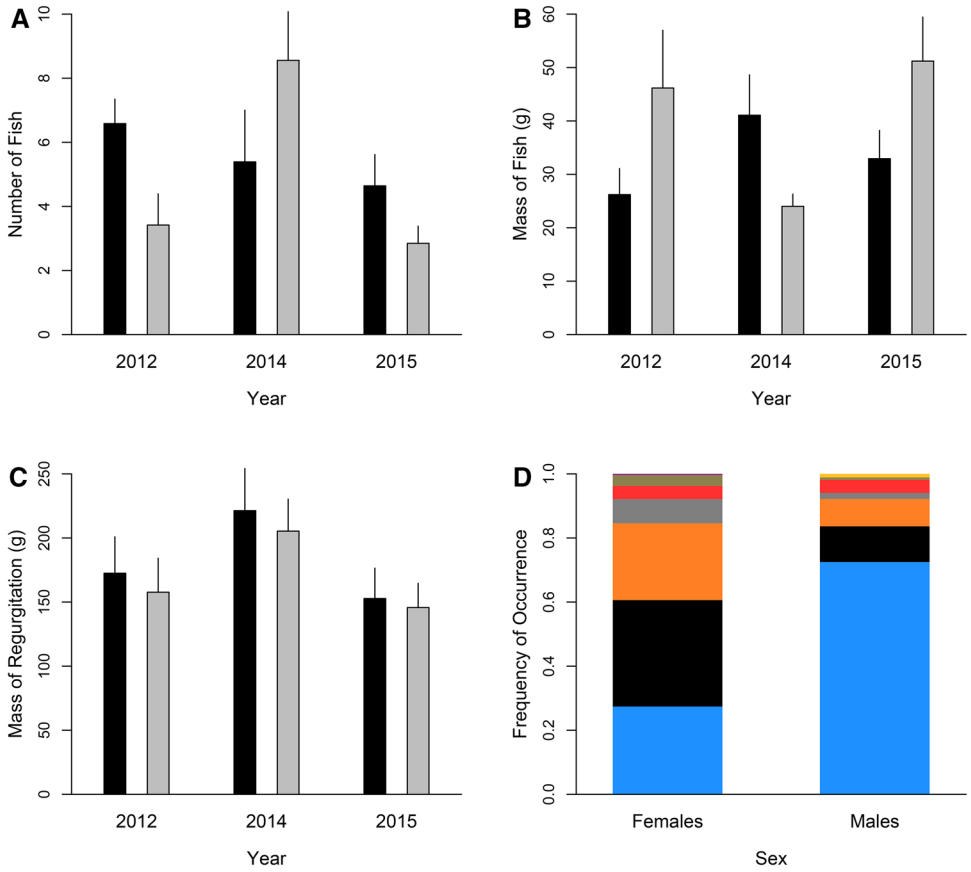

Fig. 2 **a** The mean (+SE) number of fish regurgitated by females (*black in all plots*) and males (*grey in all plots*) in each year. **b** The mean (+SE) weight of each prey regurgitated by females and males in each year. **c** The mean (+SE) total weight regurgitated by females and males in each year. **d** Across all 3 years, the proportional composition of each prey species in female and male regurgitations, by frequency of occurrence; *blue* = garfish; *black* = pilchard; *orange* = anchovy; *grey* = yellow eye mullet; *red* = squid; *brown* = yellow tail jack mackerel; *yellow* = kahawai and *purple* = barracouta

Table 2 The logit proportions of each prey species, relative garfish, as estimated (Est.) by multinomial generalized linear model in females and differences between males and females

Species	$Est._{Females}$	LCI	UCI	$Est._{Males–Females}$	LCI	UCI
Pilchard	0.193	−0.103	0.489	−2.065	−2.550	−1.580
Anchovy	−0.133	−0.454	0.187	−2.004	−2.543	−1.466
YEM	−1.291	−1.763	−0.819	−2.373	−3.378	−1.367
Squid	−1.897	−2.503	−1.290	−0.978	−1.836	−0.120
YJM	−2.079	−2.736	−1.421	−2.502	−4.043	−0.961

Those est. with a lower 95 % confidence interval (LCI) to upper 95 % confidence interval (UCI) are considered statistically significant. Note that kahawai and barracouta have not been included as they were only present in small amounts and in one sex

YEM yellow eye mullet, *YJM* yellow tail jack mackerel

S5 for full LMM output). However, for 2014, the pattern reversed with females regurgitating heavier fish than males and we also detected a significant interaction between sex and year (mass of fish $est._{Year.2014:Sex.M} \pm SE = -115.30 \pm 51.98$, $df = 101.65$, $t = -2.22$, $p < 0.05$, LMM; Fig. 2b). The mean total regurgitation mass was relatively constant (Fig. 2c), and a model containing additive effects of sex and sampling season was favoured by AICc. On average, in all years, male regurgitations weighed slightly less than female regurgitations (Fig. 2c), and the mass of the regurgitation increased slightly in 2014; however, the LM estimated no significant differences between years or sexes (see Supplementary information Table S6 for full LM output).

There were some large differences between the occurrence of each prey species in the regurgitations of male and female birds (summarized in Fig. 2d). Barracouta and kahawai were only observed in females and males, respectively, although these species occurred very infrequently (Fig. 2d). Garfish, pilchard and anchovy were the most frequently observed prey species, although in males, garfish were by far the most common (Fig. 2d). Given the prevalence of garfish in male regurgitations, we explored

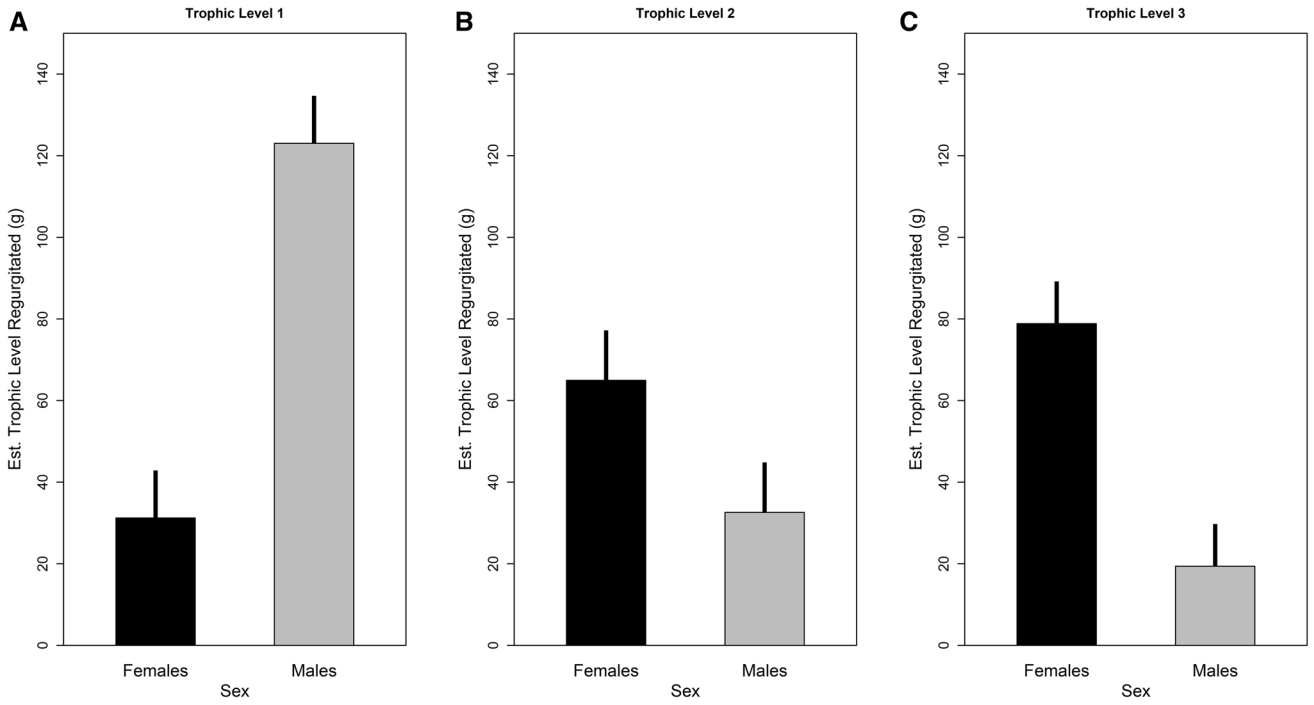

Fig. 3 The mass of fish regurgitated (g) by females and males, in an average regurgitation, belonging to **a** high trophic level, **b** medium trophic level and **c** low trophic level as estimated by linear models (Est. + SE)

differences between male and female regurgitation composition relative to this species (i.e. with garfish included as the multinomial denominator). In females, relative to garfish, pilchards and anchovies constituted similar proportions of the diet, and yellow eye mullet, arrow squid and yellow tail jack mackerel represented relatively and significantly less (Fig. 2d; Table 2). In males, garfish represented significantly larger proportions of the diet relative to all other prey species, than in females (Fig. 2d; Table 2).

On average, for a mean mass of regurgitation, females were estimated to regurgitate around 31 g of fish from the high trophic level, and males around 120 g, a difference estimated to be significantly significant (high trophic level (g) $\text{est}_{\text{Sex.M–Sex.F}} \pm \text{SE} = 91.81 \pm 16.48$, $df = 106$, $t = 5.57$, $p < 0.001$, LM; Fig. 3a and see Supplementary information Table S7 for full LM output). By way of contrast, females were estimated to regurgitate on average 65 g of fish from medium trophic level, and males only around half that amount, although this difference was non-significant (medium trophic level (g) $\text{est}_{\text{Sex.M–Sex.F}} \pm \text{SE} = -32.36 \pm 17.35$, $df = 106$, $t = -1.86$, $p = 0.065$, LM; Fig. 3b). Finally, on average, females were estimated to regurgitate around 80 g of fish from the low trophic level, and males significantly less than this (low trophic level (g) $\text{est}_{\text{Sex.M–Sex.F}} \pm \text{SE} = -59.45 \pm 14.64$, $df = 106$, $t = -4.06$, $p < 0.001$, LM; Fig. 3c).

Question 3: Does the nutritional niche in which Australasian gannets forage vary between sexes and temporally?

The lnPL (log protein-to-lipid ratio) of regurgitations was consistently positive, indicating that on average protein is more prevalent than lipid. AICc was the lowest for the model containing both sex and year, but without interaction suggesting that any seasonal changes in lnPL are not sex specific. In all years, the lnPL of males was significantly higher than that of females (lnPL $\text{est.}_{\text{Sex.Males}} \pm \text{SE} = 0.21 \pm 0.69$, $df = 107$, $t = 3.608$, $p < 0.001$, LMM; Fig. 4a, see Supplementary information Table S8 for full LMM output). In 2015, both sexes showed a significant increase in lnPL (lnPL $\text{est.}_{\text{Year.2015}} \pm \text{SE} = 0.40 \pm 0.07$, $df = 107$, $t = 5.311$, $p < 0.001$, LMM; Fig. 4a).

For lnLW (ratio of lipids to water), again a model fitting sex and sampling year as fixed predictors was favoured based on AICc. Across all years, males had a lower lnLW (ratio of lipid to water), and sex differences in this ratio were statistically significant (lnLW $\text{est.}_{\text{Sex.Males}} \pm \text{SE} = -0.21 \pm 0.06$, $df = 107$, $t = -49.80$, $p < 0.001$, LMM; Fig. 4b, see Supplementary information Table S9 for full LMM output). In addition, lnLW fluctuated across years, with the ratio being higher in 2014 relative to 2012 (lnLW $\text{est.}_{\text{Year.0.2014}} \pm \text{SE} = 0.23 \pm 0.08$, $df = 107$, $t = 2.91$, $p < 0.001$, LMM), but lower in

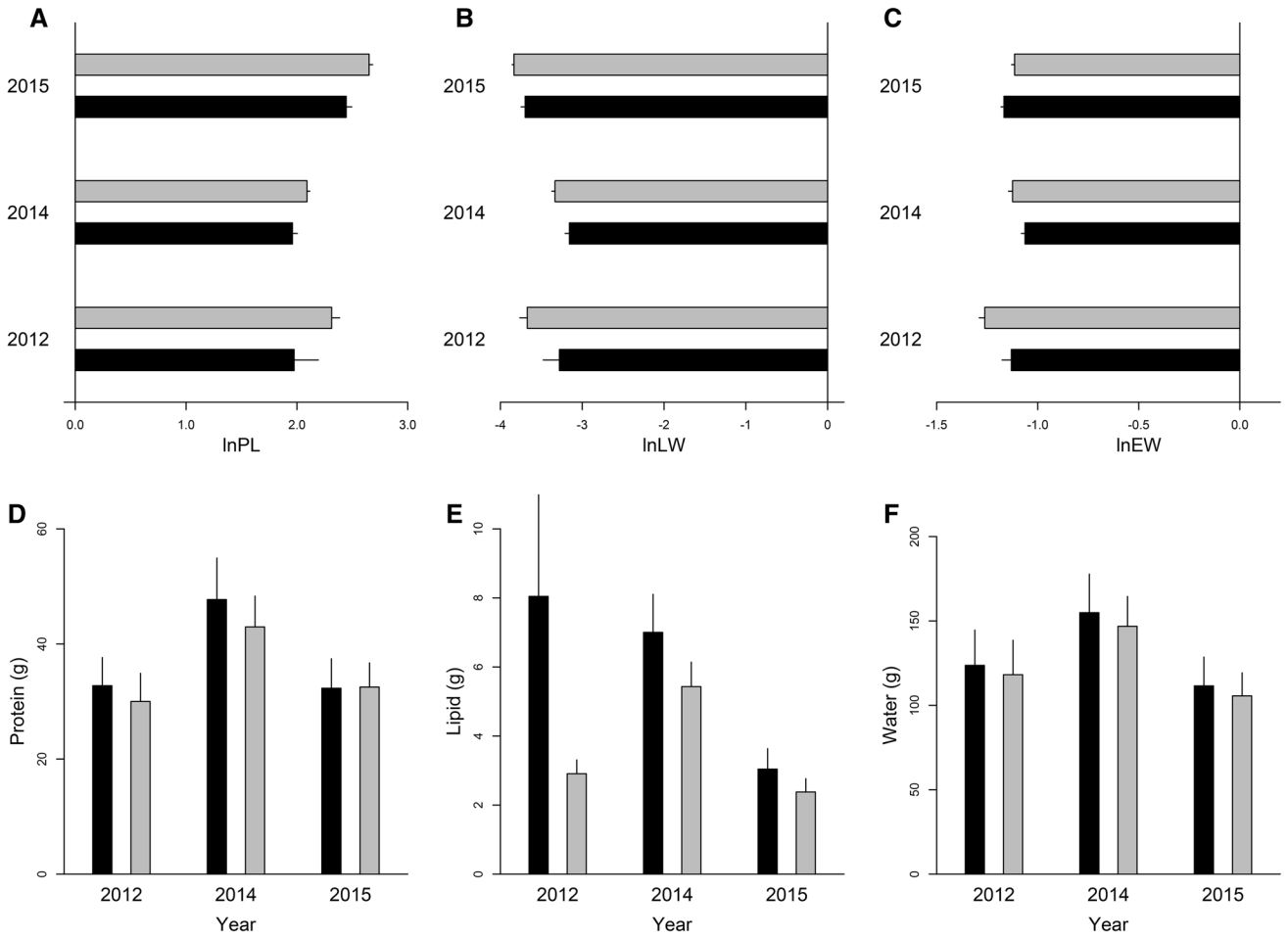

Fig. 4 Mean (+SE) **a** log ratio of protein to lipid composition (lnPL), **b** log ratio of lipids to water, **c** log ratio energy-yield to non-energy-yield components (lnE), **d** protein (g), **e** lipid (g) and **f** water (g) in regurgitations from female (*black*) and male (*grey*) gannets in each year of the study

2015 (lnLW est.$_{\text{Year.0.2015}} \pm$ SE $= -0.29 \pm 0.07$, $df = 107$, $t = -3.89$, $p < 0.001$, LMM; Fig. 4b).

The mean lnEW (log ratio of energy-yield to water) of regurgitations was consistently negative, indicating that water makes up the majority of the regurgitation (Fig. 4c), and a model fitting sex alone had the lowest AICc. The AICc model estimated that the lnEW of males was slightly but not significantly lower than females, (lnEW est.$_{\text{Sex.M}} \pm$ SE $= -0.03 \pm 0.02$, $df = 105.\ 81$, $t = 1.78$, $p = 0.08$, LMM; Fig. 4c, see Supplementary information Table S10 for full LMM output).

Despite changes in prey nutrient composition over years, and differences in their target prey species, the mean grams of protein per regurgitation was remarkably similar between males and females (Fig. 4d). There was a slight increase in the mean grams of protein from 2012 to 2014 (Fig. 4d), although this difference was non-significant (see Supplementary information Table S11 for full LMM output). A model fitting an interaction between sex and year had the lowest AICc, but no statistically significant differences between the sexes or years in mean grams protein in regurgitations were detected.

As previously stated, for the mean grams of lipid within regurgitations, a model fitting an interaction between sex and season was favoured based on AICc, but unlike for protein, there was variation between years and the sexes (Fig. 4e). In 2012, there was almost a quarter of the amount of lipid within a male regurgitation than a female regurgitation, and LMMs estimated that this difference was statistically significant [Lipid (g) est.$_{\text{Sex.Males}} \pm$ SE $= -5.14 \pm 2.41$, $df = 105$, $t = -2.13$, $p < 0.05$, LMM; Fig. 4e, see Supplementary information Table S12 for full LMM output]. In 2014, females showed lower mean grams of lipid in their regurgitation than males, although the model did not detect a significant difference between 2012, or significant interaction between year and sex. In 2015, the grams of lipid per regurgitation by females was approximately half that of 2012, a difference that was

statistically significant (lipid (g) $est._{Year.2015} \pm SE = -5.00 \pm 2.08$, $df = 105$, $t = 1.14$, $p < 0.05$, LMM; Fig. 4e).

Finally, the water content of regurgitations was relatively constant across years and sexes (Fig. 4f). The LMM fitting an interaction between sex and year had the lowest AICc. Despite the water content of females being slightly higher than that of males across years, we detected no significant effect of sex or year (see Supplementary information Table S13 for full LMM output).

Discussion

Understanding the mechanisms governing the dietary choices of wild carnivores is fundamental to understand the evolution and adaptations of predators, as well as their roles in structuring ecological communities (Wilder and Eubanks 2010; Simpson and Raubenheimer 2012). Macronutrient requirements, food selection and dietary intake are likely to differ between sexes due to physiological differences and post-ingestive nutrient processing (Maklakov et al. 2008; Morehouse et al. 2010; Senior et al. 2015). Considerable progress has been made towards understanding diet, macronutrient selection and the effects thereof on sex-specific traits by studying several predators under laboratory conditions, including mink (*Mustela vison*, Mayntz et al. 2009), wolf spiders (*Pardosa amentata* and *Pardosa prativaga*, Jensen et al. 2011) and beetles (*Agonum dorsale*, Mayntz et al. 2005; Raubenheimer et al. 2007; and *Achnomenus dorsalis*, Jensen et al. 2012). However, evidence for sex-specific macronutrient selection in wild carnivores is limited. Our study therefore helps to fill this knowledge gap, providing detailed quantifications of the differences between foraging and nutritional strategies of the sexes of a successful marine predator, the Australasian gannet, in a fluctuating and complex nutritional environment.

Foraging in a complex marine nutritional environment

Abiotic and biotic factors are well known to affect the abundance, distribution and quality of marine food sources, with subsequent impacts on the breeding success of marine predators (Österblom et al. 2008; Paiva et al. 2013). Our results demonstrate that Australasian gannets forage in a nutritionally complex and fluctuating marine environment. We found intra- and inter-specific variation in the protein, lipid and water composition of the prey captured by Australasian gannets. For example, the average log ratio of protein to lipid in garfish was 29.7 % higher in 2015 than in 2014. These results support previous findings in this species (Tait et al. 2014) and also emphasize the nutritional variability of prey consumed by marine predators (Wanless et al. 2005; Spitz et al. 2010; Lenky et al. 2012), and draws into question the long-term assumption that wild predators feed on prey that are similar in their nutritional composition (Westoby 1978; Stephens and Krebs 1986; Galef 1996).

Vertebrates are well known for their ability to balance their diet from multiple nutritionally differing foods in order to reach an optimal nutrient intake (Raubenheimer and Simpson 1997), and also for their ability to adapt to changes in the availability of high-quality prey within their environments (Hailey et al. 1998). Our nutritional models (RMT) showed seasonal variation in diets and nutritional niches in which gannets forage. Presumably such temporal fluctuations are not solely limited to the years in which we have sampled, but have also happened regularly in the past. Despite such temporal variation, the gannet colony at FS has shown continuous growth (Schuckard et al. 2012). Our findings may thus be seen as further evidence of this species' ability to successfully adjust to nutritional fluctuations of prey (Grémillet et al. 2008; Tait et al. 2014). In addition, during the three breeding seasons, adult chick-rearing Australasian gannets consistently composed around 80 % of their diet from three different types of prey. It has been suggested that predators are fundamentally driven by the goal of maximizing energy intake and therefore have no need to select nutritionally complementary prey to balance their diet (Stephens and Krebs 1986; Galef 1996; Fryxell and Lundberg 1997). Our results showed that Australasian gannets consumed prey that substantially differs in their protein-to-lipid ratio from 1.5:1.0 (barracouta) to 15.5:1.0 (garfish), suggesting that marine predators forage in an environment in which nutritionally complementary prey are available. However, our evidence suggests that foraging Australasian gannets were likely to mix supplementary foods that had a similar macronutrient balance, rather than combine complementary foods with disparate compositions.

Sex-specific macronutrient differences

In breeding organisms, despite sharing similar genomes, each sex must use different strategies to convert their food choices into reproductive outputs (Morehouse et al. 2010). Gannets use the first portion of their foraging trips to feed themselves, before capturing food for their chicks and returning to the breeding site (Hamer et al. 2000; Ropert-Coudert et al. 2004). We found that females and males bring similar amounts of foods to chicks (in terms of mass), which contrasts with previous suggestions that female gannets are likely to be the main food supplier to the offspring (Montevecchi and Porter 1980; Montevecchi et al. 1984). Our results also showed that males more consistently prey upon garfish, foraging at the highest possible trophic level, whereas females combined similar proportions of garfish, pilchard and anchovy in their diets while foraging

predominantly at lower trophic levels. These results are consistent with previous findings in three different species of gannets (Lewis et al. 2002; Bijleveld and Mullers 2009; Mullers and Navarro 2010; Ismar 2010).

Sex-specific prey selection in the wild may be linked to the nutrient-specific requirements of each sex and/or their progeny, although field-based evidence is rather limited. Nutritional ecology provides the appropriate framework to address the causes and consequences of nutritional differences, from food selection and nutrient processing to sex-specific reproductive traits (Raubenheimer et al. 2009; Morehouse et al. 2010). Our data on the nutritional composition of regurgitations between sexes revealed that males consumed diets with higher protein-to-lipid ratios and lower lipid-to-water ratios than females. These results are consistent with previous suggestions that gannet foraging behaviour is likely to be linked to sex-specific nutrient needs (Lewis et al. 2002). Based on our findings, three non-exclusive hypotheses may be suggested. First, in marine prey species water content varies inversely proportional to lipid content among seasons and locations (Montevecchi and Piatt 1984). Our results suggest that males and females bring nutritionally imbalanced foods to the nest, but when combined allow the offspring to reach its multidimensional nutritional target of protein, lipid, water and micronutrients (Montevecchi and Porter 1980; Montevecchi et al. 1984; Morehouse et al. 2010). In this case, adults' nutritional needs are likely to influence foraging behaviour (diving, foraging trip durations and habitat use), such that different sexes will exploit vertical and horizontal habitats to capture certain foods that enable them to attain specific nutrients (Lewis et al. 2002; Cleasby et al. 2015). Gannets have characteristic pair-greeting ceremony behaviour as part of the changing guard at the nest, known as bill fencing (Nelson 1978). Although there is no evidence supporting the use of these ceremonies as a source of private information (Machovsky-Capuska et al. 2014b), a possible functional role for them is providing feedback on the nutritional state (e.g. body condition, colouration) of the foraging partner, although this theory is yet to be tested.

A second hypothesis may be related to the body condition and physiological challenges that females and males face in processing nutrients (Duke 1997). Digestive efficiency and retention time of nutrients directly influence foraging behaviour and maximum food intake rate; therefore, small differences in the physiology of the sexes may translate into larger impacts on foraging decisions (Hilton et al. 2000). Previous work has noted an apparent ability of female vertebrates to metabolize proportionally more lipids than males (Tarnopolsky and Saris 2001). However, it remains to be explored whether the adult's body condition and the ability to metabolize different nutrients influence the nutritional quality of foods selected for chicks.

A third hypothesis relates to whether the chicks' appearance (e.g. changes in body mass and physiological condition) influences adults' foraging strategies and macronutrient consumption in the foods that are brought to the nest. It has been suggested that most seabird parents continuously provide high concentrations of lipids to the chicks as insurance against temporal or spatial variation in food supply (Ricklefs 1990). However, many procellariiform seabirds are known for using short and long foraging trips that provide different food quality to the chicks, suggesting a possible link between life history traits and foraging strategies (Weimerskirch et al. 1994; Stahl and Sagar 2006; Magalhães et al. 2008). In most seabird species, including gannets, vision is fundamental for communication, foraging and reproduction (Machovsky-Capuska et al. 2011b, 2012). During their development, chicks show visual age-related changes such as feather appearance, wing development and also the end of lean tissue growth that has been presumably indicative of a reduction in their nutrient requirements (Phillips and Hamer 1999). Thus, it is possible that parents are able to assess their chicks' nutritional requirements prior to their departure for foraging. However, this requires further exploration.

By combining dietary analyses and nutritional geometry, we provided detailed quantifications of the effects of sex-specific foraging strategies on parental macronutrient provisioning in a successful marine predator in the wild. We have shown that in spite of the constant fluctuations in the nutritional composition of foods available to Australasian gannets, males consistently capture prey with higher protein-to-lipid ratios and lower lipid-to-water ratios than females. Our results help to better understand the evolutionary relationship between macronutrient selection and sexually dimorphic traits in wild animals. In addition, we also suggest that predators should be able to combine nutritionally imbalanced, but complementary foods, and thus also that prey selection by wild predators is likely to be guided by specific nutrient content, rather than just by the energetic value of prey.

Data accessibility

Data and coding are currently deposited on Pangaea® Repository.[1]

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Author contributions G. E. M.-C., E. B., W. C., D. M., R. S., K. B., C. P. and M. O. collected the data. A. M. S., G. E. M.-C., E. B., C. P., A. H. T., W. C., B. W., K. B. and D. R. analysed the data. G. E. M.-C., A. M. S., E. B., A. H. T., D. M., C. P., M. O., B. W., K. A. S. and D. R., wrote and edited the manuscript. G. E. M.-C., D. R. and K. A. S. designed the study.

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