Marine Biology (2019) 166:121
https://doi.org/10.1007/s00227-019-3570-9

ORIGINAL PAPER

Forage fish to growing chicks: shared food resources between two closely related tern species

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Received: 3 April 2019 / Accepted: 17 August 2019 / Published online: 30 August 2019

Abstract

The assessment of the relevance of forage fish in seabird diet and how different species partition food resources is fundamental to understand predator–prey relationships. We assessed the importance of forage fish in the diet of Royal (*Thalasseus maximus maximus*) and Cayenne (*T. sandvicensis eurygnathus*) terns and their partitioning of food resources during the early and late chick stages of 2013 and 2014 at a colony in Argentina. Direct observation of prey deliveries during chick provisioning showed that diet composition of Royal and Cayenne terns comprised at least 16 and 9 prey species, respectively. In both tern species, Argentine Anchovy (*Engraulis anchoita*) and five species of silversides (*Odontesthes spp.*) were the main prey fed to chicks (over 90% contribution, anchovy and silversides pooled). Both tern species fed their chicks with similar prey species, but Royal terns delivered, in general, larger prey than Cayenne terns. Based on carbon and nitrogen isotopic values from chick whole blood samples, Bayesian mixing models showed that anchovies and silversides contributed similarly to the diet of both tern species' chicks. Both conventional and stable isotope methods showed a high overlap in their trophic niches. Prey sizes delivered to chicks were larger in the late chick stage and the second study season. Wind speed did not have a significant effect on the frequency of the different prey species and sizes delivered to chicks by both tern species. As anchovies and silversides are fishery targets, tern trophic requirements should be considered when planning future fisheries development and management.

Introduction

Low trophic level pelagic fish species, termed forage fish, play a critical role in marine ecosystems feeding on plankton and transferring energy to higher trophic levels (Pikitch et al. 2012). They are key prey for many seabirds, marine mammals and larger fish species, and are often targeted by commercial fisheries worldwide (Pikitch et al. 2012). Several studies have shown that forage fish availability may have significant effects on seabird breeding success and individual survival (e.g. Crawford and Dyer 1995; Cury et al. 2011). In this context, the assessment of the relevance of forage fish in seabird diet requirements is fundamental to the understanding of predator–prey relationships and the assessment of potential conflicts with fisheries.

Like many other seabirds, terns of the genus *Thalasseus* depend on forage fish during the breeding season (Crawford and Dyer 1995; Gatto and Yorio 2009) and often nest in mixed-species breeding assemblages including other tern species (Hulsman 1988; McGinnis and Emslie 2001; Yorio and Efe 2008). Several seabird studies have shown that a difference in prey selection is one of the mechanisms that allows the coexistence of different seabird species at the same breeding location, and both species and size of prey may be involved in dietary segregation (Ashmole and Ashmole 1967; Wiens 1989; Robertson et al. 2014). Seabirds are central place foragers during the breeding season, commuting between foraging areas and nests sites to incubate their eggs or feed their chicks, and in species such as terns, they are restricted to exploit resources within a limited range around their colonies (Orians and Pearson 1979). In this context, resource partitioning may increase during periods

Responsible Editor: V. H. Paiva.

Reviewed by D. Gaglio and undisclosed experts.

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of increased energy demand such as the chick-rearing stage when they have to obtain prey for self-feeding and chick provisioning (Barger et al. 2016).

As with most seabirds, the use of food resources by terns may depend on factors such as changes in food availability and individual requirements (Stienen et al. 2000; Fernández Ajó et al. 2011). In particular, diet composition can change in relation to chick age, because of changing energetic requirements and the greater difficulty of small chicks to manipulate and swallow large prey (Hulsman 1981; Shealer 1998; Wambach and Emslie 2003). Terns are surface-feeders restricted to obtain food from the top layer of the water column, and factors such as wind speed may determine diet composition by affecting both prey accessibility and foraging behaviour (Stienen et al. 2000; Paiva et al. 2006).

Royal and Cayenne terns (*Thalasseus maximus maximus* Boddaert, 1783 and *T. sandvicensis eurygnathus* Latham, 1787, respectively) are two widely distributed coastal species in the Americas (Buckley and Buckley 2002; Shealer et al. 2016). Royal and Cayenne terns show important differences in body size, with the former being almost twice as heavy (Lisnizer et al. 2014), and they often nest in mixed-species colonies along the coasts of Argentina, Uruguay and Brazil (Yorio and Efe 2008; Lenzi et al. 2010). Both species show similar breeding patterns and foraging strategies (Quintana and Yorio 1997; Gatto and Yorio 2009). The little information available on the breeding diet requirements of Royal and Cayenne terns in the Southwest Atlantic coasts indicates that both species mainly consume forage fish from the Engraulidae and Atherinopsidae families (Gatto and Yorio 2009; Fracasso et al. 2011). A study on the coast of northern Patagonia, Argentina, showed that the diet of both was comprised of Argentine Anchovy (*Engraulis anchoita* Hubbs and Marini, 1935) and two species of silversides (*Odontesthes* spp.), with Royal terns feeding mainly on Argentine Anchovy and Cayenne terns on silversides (Gatto and Yorio 2009). Trophic relationships between syntopic *Thalasseus* terns in other regions also indicate that tern species partition prey resources (Hulsman 1988; McGinnis and Emslie 2001).

Diet studies using conventional diet methods, such as stomach content analysis and direct observations of prey deliveries during chick provisioning provide detailed information on prey species composition but only from the last feeding event. On the other hand, stable isotope analysis of blood provides information on the consumption of the main prey species over a larger temporal scale but may be inadequate for estimating the fine-scale taxonomic composition of seabird diet. The combination of conventional and biochemical methods is often recommended to overcome some of their respective limitations, minimize biases, and adequately assess diet requirements (Karnovsky et al. 2012). In addition to providing information on the ecological requirements of both species, their relationship to forage fish, and on how these closely related terns partition prey resources, diet information can contribute with valuable baseline data for the future assessment of seabird–fisheries interactions in the region. Argentine Anchovy is the most abundant and ecologically important pelagic fish resource off Argentina, and the northern stock is the target of commercial trawl fisheries (Hansen et al. 2001). Silversides of the genus *Odontesthes* are also ecologically relevant as forage fishes and economically significant for artisanal and recreational fisheries in the Southwest Atlantic (Chao et al. 1985; Llompart et al. 2012).

In this study, we (1) assessed the importance of forage fish in the diet of Royal and Cayenne terns during two breeding seasons in the Bahía San Blas protected area, (2) assessed food partitioning between the two tern species in terms of the type and size of prey delivered, and (3) assessed the effect of wind speed on chick diet composition. We expected that Royal and Cayenne terns would differ in the size of prey fed to chicks, with the larger Royal Tern delivering larger prey. We also expected that diet composition in terms of prey type and size would change between chick stages given the fluctuations generally found in forage fish populations and the requirements of growing chicks (Shealer 1998; Pikitch et al. 2012), and that prey delivered would differ between different wind speeds (Paiva et al. 2006).

Materials and methods

Study area

The study was conducted in the southwestern sector of the Bahía San Blas Multiple Use Nature Reserve in Buenos Aires Province, Argentina, which includes terrestrial and marine environments characterized by extensive mudflats, marshes and channels with several islands, islets and banks (Zalba et al. 2008). The town of Bahía San Blas, of about 600 inhabitants, is located in Isla del Jabalí (40°33′S, 62°14′W). The main economic activity in the area is recreational fishing (Zalba et al. 2008), targeting mainly Stripped Weakfish (*Cynoscion guatucupa* Cuvier, 1830), Whitemouth Croaker (*Micropogonias furnieri* Desmarest, 1823), Narrownose Smooth Hound (*Mustelus schmitti* Springer, 1939) and silversides (mainly *Odontesthes argentinensis* Valenciennes, 1835 and *O. platensis* Berg, 1895) (Llompart 2011). The area receives an average of over 40,000 recreational fishers per year, mostly during the spring and summer months, both shore- and boat-based (about 40 licensed fishing boats) (Llompart 2011). Recreational and artisanal fishing are allowed in some sectors of the protected area, including the area covered in the present study. Royal and Cayenne tern diet composition was analysed during the 2013 and 2014 breeding seasons at a mixed-species colony located in Banco

Nordeste (40°32′S, 62°10′W), consisting of an estimated 840 and 195 nests, respectively (Suárez et al. 2014). Both tern species start laying in mid-October, eggs start hatching in mid-November and chicks fledge in mid-December.

Conventional diet sampling

Diet composition of Royal and Cayenne terns was determined using direct observations of prey deliveries to their chicks (Barrett et al. 2007). Some studies have highlighted the potential problems when determining through direct observations the prey captured or delivered by birds to their chicks (Cezilly and Wallace 1988; Gaglio et al. 2016). However, the conditions under which observations were made in this study allowed the identification of prey species with a high degree of confidence. In each breeding season, a patch of ~150 nests was selected to conduct focal observations. Sampling was conducted during a total of 10 non consecutive days during 2013 (52 h) and 9 non consecutive days during 2014 (42 h), split in two stages of the chick-rearing period, the young chick stage (< 15 days of age; small chicks completely covered with down; November 17–22 in 2013 and 18–22 in 2014) and the old chick stage (≥ 15 days of age; large chicks with at least part of the body with visible growing feathers; November 30–December 3 in both study years). Observations were made between 08:00 and 21:00 h, distributed among one to three observation periods lasting 2–3 h and encompassing different stages of the tidal cycle and weather conditions.

Feeding observations were made for the two tern species simultaneously. Both species carry only one prey item in the bill per trip back to their nests. Observations were carried out from a blind located at the periphery of the tern colony. The blind was positioned very close to the birds, allowing the detection of even small differences among prey species. Adults attempting to land at the study patch with prey were continuously scanned. Once an adult carrying a prey was selected, it was observed with binoculars until the prey could be identified, often while the adult was attempting to feed its chick. Provisioning terns in general circle the nest, land, fly away and circle again before finally feeding their chick, so there was sufficient time for prey identification. As terns may land and take off again with their prey, possible pseudoreplication was kept to a minimum by noting the landing nest and the prey position in the bill (orientation of tail or abdomen) (Gatto and Yorio 2009). Photographs and video footages were taken for cases in which there were difficulties in identifying prey carried by approaching terns (< 1%) (Larson and Craig 2006; Gaglio et al. 2016), which later allowed confirmation of species assignment. All prey items were identified to the lowest taxonomic level possible using morphological characters (Menni et al. 1984). As there are no English common names for each of the silverside species found in the study area, different letters were assigned to the different species to standardize the presentation of results. Given the great similarity between the species *O. argentinensis* and *O. platensis*, individuals of these species were assigned to the category "Silverside A". Most silverside individuals smaller than 70 mm could not be determined to species, as those sizes correspond to juvenile age classes (Bovcon 2016) and these are morphologically very similar among species. Therefore, they were assigned to the category "juvenile silversides" (*Odontesthes* spp.). Due to their morphological characteristics, smaller sized anchovies were easily distinguishable from the rest of the species in the area (Ciechomski 1981; Menni et al. 1984). Prey length was noted relative to the bill-length of the adult. The size of prey was categorized as 'tiny' (< 0.5 × bill-length), 'small' (0.5–1.0×), 'medium' (1–1.5×), 'large' (1.5–2.0×) and very large (> 2.0×). Bill-length of adult Royal Terns is 64 ± 3 mm and that of Cayenne terns is 59 ± 3 mm (Lisnizer et al. 2014). Feeding observations and estimations of length of prey in both breeding seasons were made by only one observer (*C. Marinao*) to reduce observer bias in determination of prey species and sizes. In each observation period, wind speed (km/h) was obtained every 15 min from a meteorological station located near the tern colony. Wind speed was variable throughout the chick stage with peaks of up to 49 km/h, although it was in general of moderate intensity (mean: 26.6 ± 9.17 km/h, range 6.5–49.0 km/h).

The effects of tern species, chick stage, breeding season and wind speed on the frequency of delivery of the Argentine Anchovy and silversides were evaluated using generalised linear models (GLM) with a binomial error structure and logit link function, as statistical assumptions of normality were not met (Faraway 2006). Wind speed values included in the model were the mean wind speed for each hour of the observational bout. Model selection procedures were based on information theory (Burnham and Anderson 2002). This method allows for the inclusion of model uncertainty both in its evaluation and in the estimation of parameters (Burnham and Anderson 2002). Models with all possible combinations of predictor variables were considered and best-fitting models were selected using Akaike's Information Criterion (AIC). Ordered logistic regressions (OLRs) (Agresti 2002) were used to assess the effects of the tern species, chick stage and breeding season on the size of prey delivered. GLMs and OLRs were fitted using the R program version 3.3.1 (R Development Core Team 2016). For both the GLM and OLR analyses, the five species of silversides were grouped into a "silversides" category due to their similar morphological and ecological characteristics. Prey richness was defined as the observed number of prey species, and prey diversity was calculated using the Shannon Diversity Index (Krebs 1999). Unidentified prey (0.16% of 8140 feeding observations) were not included in the former analyses. The overlap between tern species in prey type and fish length was estimated using the Czechanowski index as a measure of niche overlap (Krebs 1999).

Stable isotope analysis

Stable isotope analysis was conducted to complement the information obtained through direct observations of prey delivered to chicks. Whole blood samples were collected in 2014 to assess the carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic composition that reflected the diet of Royal and Cayenne tern chicks of over 20 days of age ($n = 10$ for each tern species), distinguished by size and the degree of plumage development (*C. Marinao*, unpublished data). Whole blood was used because it integrates the isotopic composition of prey ingested by an individual during approximately 3 weeks before sample collection (Hobson and Clark 1992). Blood samples (0.5–1 ml) were extracted from the brachial vein of each individual and preserved in 70% ethanol. When freezing is not available, blood preservation in 70% ethanol has been recommended as it has no significant effects on the isotopic values of the blood (Hobson et al. 1997), although this may not be the case in all situations (Bugoni et al. 2008). Main prey items in the diet of both tern species (Argentine Anchovy and Silverside B *O. nigricans* Richardson, 1845) were used in the isotopic mixing models, and were selected based on preliminary diet information obtained in 2012 and the results of this study. Prey individuals in the range of sizes consumed by terns were collected using a landing net in 2014 in the study area. Muscle tissues were extracted and kept frozen until analysis. Samples of adult and juvenile Argentine Anchovies were processed ($n = 10$) and lipids were extracted using chloroform–methanol (2:1) (Post et al. 2007). No differences in stable isotope values of juvenile and adult Argentine Anchovy were found ($P > 0.05$), so they were pooled for analysis. Among silversides, only individuals of "Silverside C" (*O. smitti* Lahille, 1929) could be obtained from fresh regurgitated prey found within the colony ($n = 5$). Given the similarity in the trophic niche of individuals of Silverside C and other silversides species and among individuals within the range of sizes consumed by terns (Irigoyen et al. 2018; N. Bovcon, pers. comm.), isotopic values of the former were used. Blood and muscle samples were dried at 60 °C over 24 h and then ground in a micro-mortar. A subsample of 1 ± 0.2 mg of tern blood and prey muscle was set in a tin capsule for stable isotope analysis. Sample analyses were performed by the Stable Isotope Facility of the University of California at Davis (USA). Stable isotope abundance is expressed using standard δ notation relative to carbonate Vienna Pee Dee Belemnite and atmospheric nitrogen. The internal laboratory standards used were Bovine Liver, USGS-41 Glutamic Acid, Nylon 5 and Glutamic Acid. Observed analytical errors were 0.14‰ and 0.19‰, for δ^{13}C and δ^{15}N, respectively.

For each tern species, the relative contribution of Argentine Anchovy and silversides to the isotope mixture was analysed using the R package SIMMR (Parnell et al. 2013). Two mixing models were ran, one for each tern species, using in each model the isotopic composition of individuals. Differences between tern species in the contribution of Argentine Anchovy and silversides were tested using the same R SIMMR package. Before running the isotopic mixing models, a sensitivity analysis was conducted using a slightly modified version of the method proposed by Smith et al. (2013) to evaluate the feasibility of the proposed isotopic mixing polygon. As there are no diet-tissue discrimination factors (DTDFs) available for Royal and Cayenne terns, the values of DTDFs between prey and whole blood of the Great Skua (*Catharacta skua*) were used following Bearhop et al. (2002) (1.1‰ for δ^{13}C and 2.8‰ for δ^{15}N). Although published information on DTDFs of piscivorous seabirds is scant, it is likely they are qualitatively similar between species (Bodey et al. 2014). A standard deviation of ± 0.3‰ was added to both DTDFs values to account for potential differences in discrimination factors between actual values for Royal and Cayenne terns and those used in that study. This value was estimated as the mean dispersion of DTDFs of Charadriiformes reported in Bond and Diamond (2011). The isotopic composition of Argentine Anchovy was $\delta^{13}\text{C} = -18.7 \pm 0.5$‰, $\delta^{15}\text{N} = 16.1 \pm 0.7$‰, and for Silverside C $\delta^{13}\text{C} = -19.1 \pm 1.3$‰, $\delta^{15}\text{N} = 14.5 \pm 0.7$‰. Isotopic niches were compared using the hypothesis-testing framework proposed by Turner et al. (2010) and the approach based on multivariate ellipse metrics (Jackson et al. 2011). Differences in centroid location, which provide information on isotopic position, and eccentricity, which provides insight into differences in the underlying distribution of δ^{13}C and δ^{15}N data, were tested using nested linear models and residual permutation procedures (see Turner et al. 2010 for statistical details). To describe the spread of data points, parameters that provide insight into differences in the underlying distribution of δ^{13}C and δ^{15}N data, such as mean distance to centroid, mean nearest-neighbour distance and eccentricity, were calculated (Layman et al. 2007; Turner et al. 2010). Differences were tested following the methodology proposed by Turner et al. (2010). The isotopic niche width for each tern species was estimated using multivariate ellipse-based metrics (Jackson et al. 2011). The analysis generates standard ellipse areas (SEA) which are bivariate equivalents to standard deviations in univariate analyses. SEA values corrected for small sample size (SEA_C) were used to calculate niche overlap and Bayesian estimates of SEA (SEA_B) were generated to test differences in isotopic niches between tern species by comparing their 95% credible intervals (CI) (for examples see Jackson et al. 2012; Thomson et al. 2012; Gatto and Yorio 2016). Mean values were reported ± 1 SD.

Results

Direct observations

A total of 8140 prey deliveries by Royal and Cayenne terns were recorded in both breeding seasons (Royal Tern: $n = 3877$; Cayenne Tern: $n = 4263$). The diet of Royal Tern chicks was comprised of almost exclusively fish corresponding to 11 families, represented by at least 13 species from pelagic, demersal and benthic habitats (Table 1). Only one unidentified invertebrate species was recorded in both breeding seasons, although in very low frequencies (< 0.5%). In 2013, Argentine Anchovy dominated diet composition during the young chick stage (78.4%) while during the old chick stage the higher frequencies corresponded to Argentine Anchovy (24.7%) and Silverside A (23.5%) (Table 1). The most frequent prey during the young chick stage in 2014 were juvenile silversides (27.2%), Argentine Anchovy (25.8%) and Silverside D (*O. incisa* Jenyns 1842) (24.5%), while the most frequent in the old chick

Table 1 Frequency of occurrence (%) of prey delivered to chicks by Royal and Cayenne terns during the young and old chick stages (< 15 and ≥ 15 days of age, respectively) of the 2013 and 2014 breeding seasons at Banco Nordeste, Argentina

Prey	Royal tern				Cayenne tern			
	2013		2014		2013		2014	
	YC	OC	YC	OC	YC	OC	YC	OC
	($n = 1770$)	($n = 693$)	($n = 802$)	($n = 612$)	($n = 1483$)	($n = 1033$)	($n = 1042$)	($n = 705$)
Engraulidae								
Argentine Anchovy (*Engraulis anchoita*)	78.3	24.7	25.8	27.1	85.3	41.3	29.7	32.6
Atlantic sabertooth anchovy (*Lycengraulis grossidens*)	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Atherinopsidae								
Juvenile silversides (*Odontesthes* spp.)	2.8	13.3	27.2	11.9	2.8	25.9	31.5	19.9
Silverside C (*O. smitti*)	12.4	17.5	6.2	0.8	9.7	14.4	10.5	0.3
Silverside A (*O. argentinensis/platensis*)	3.4	23.5	4.2	16.8	1.3	9.7	1.2	6.1
Silverside B (*O. nigricans*)	0.0	13.4	3.9	29.9	0.0	5.8	5.6	34.0
Silverside D (*O. incisa*)	0.0	2.4	24.4	4.2	0.0	1.6	18.1	5.1
Clupeidae								
Jenyns's sprat (*Ramnogaster arcuata*)	1.5	2.3	7.5	5.2	0.8	1.1	3.7	1.7
Scianidae								
Stripped weakfish (*Cynoscion guatucupa*)	0.0	0.0	0.1	2.4	0.0	0.0	0.0	0.1
Stromateidae								
Butterfish (*Stromateus brasiliensis*)	0.0	0.0	0.0	0.2	0.0	0.1	0.0	0.0
Carangidae								
Parona leatherjack (*Parona signata*)	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Percophididae								
Brazilian flathead (*Percophis brasiliensis*)	0.3	0.1	0.0	0.6	0.0	0.0	0.0	0.0
Pleuronectidae								
Pleuronectiformes	0.4	0.6	0.0	0.0	0.0	0.0	0.0	0.0
Batrachoididae								
Toadfish (*Porichthys porosissimus*)	0.3	1.3	0.1	0.0	0.0	0.0	0.0	0.0
Scombridae								
Chub mackerel (*Scomber japonicus*)	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Invertebrates	0.3	0.1	0.1	0.2	0.0	0.0	0.0	0.0
Unidentified fish	0.0	0.0	0.1	0.5	0.0	0.0	0.0	0.0
Unidentified	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.1
Species richness	9	13	9	10	5	8	7	8
Diversity	0.7	1.6	1.6	1.6	0.5	1.3	1.5	1.3

YC young chicks, *OC* old chicks

stage were silverside B (29.9%) and Argentine Anchovy (27.1%). Cayenne Tern diet was comprised of exclusively fish belonging to five families, represented by at least eight species (Table 1). During 2013, Argentine Anchovy was the dominant prey species in the young chick stage (85.4% of which 99.5 were juveniles) and the main component in the old chick stage (41.3% of which 99.3% were juveniles), followed by the unidentified silverside category (25.9%) (Table 1). The highest frequencies during the young chick stage of 2014 corresponded to juvenile silversides (31.5%) and Argentine Anchovy (29.7%, of which 90.7% were juveniles), while the highest frequencies during the old chick stage corresponded to Silverside B (34.0%) and Argentine Anchovy (32.6%, of which 76.6% were juveniles). Species richness and diversity in Royal terns varied between 9 and 13 and between 0.7 and 1.6, respectively, depending on breeding stage and year (Table 1). In Cayenne terns, species richness and diversity varied between 5 and 8 and between 0.5 and 1.5, respectively, depending on breeding stage and year (Table 1). Based on the observations of prey deliveries, the overlap between the trophic niche of Cayenne and Royal terns was high (Czekanowski Index: 0.85).

Argentine Anchovy and silversides were the main prey in all chick stages and breeding seasons for both tern species (Table 1). The best model explaining the variation in the frequency of Argentine Anchovies and silversides delivered to their chicks by both tern species included tern species, chick stage, breeding season and the interaction between the last two (Table 2a). Wind speed did not have a significant effect on prey delivered by both tern species (Table 2a). Model parameters indicated that Royal Terns delivered to their chicks a lower proportion of Argentine Anchovy than Cayenne terns (GLM, $\beta = -1.2$, $z = -12.0$, $d.f. = 1$, $P < 0.0001$). However, there was an interaction between chick stage and breeding season indicating that the proportion of Argentine Anchovies and silversides delivered in a certain stage depended on the breeding season (GLM, $\beta = 0.61$, $z = 2.8$, $d.f. = 1$, $P = 0.005$). Both tern species delivered to their chicks a higher proportion of Argentine Anchovies in 2013 but a higher proportion of silversides in 2014 (Table 1). Similar results were found when the effects of factors were analysed for each species of tern separately (Table 2b, c).

In 2013, the larger Royal terns delivered mainly tiny fish during the young chick stage (60.4%) and large, medium and tiny fish during the old chick stage (30.9, 29.6 and 25.7%, respectively) (Fig. 1). In 2014, Royal terns delivered mainly small and medium prey in the young chick stage (37.5 and 35.3%, respectively) and medium sized and large prey during the old chick stage (29.1 and 34.31%, respectively) (Fig. 1). In 2013, Cayenne terns delivered mainly tiny fish during the early chick stage (79%) and small and tiny fish during the old chick stage (53.3 and 24.8%, respectively) (Fig. 1). In 2014, parents delivered mainly small prey in the young chick stage (41.8%) and small- and medium-sized prey during the old chick stage (33.3 and 31.6%, respectively) (Fig. 1).

When both tern species were analysed together, the best model describing the variation in prey size included the effect of tern species, prey type, chick stage, breeding season and the interaction between the last two (Table 3a). Model parameters indicated that Royal terns delivered to their chicks larger prey than Cayenne terns (ORLs, $\beta = 0.9$, $z = 20.1$, $d.f. = 1$, $P < 0.0001$). The size of Argentine Anchovies delivered by both tern species was significantly smaller than that of silversides (ORLs, $\beta = -2.6$, $z = 44.5$, $d.f. = 1$, $P < 0.0001$). There was an interaction between stage and breeding season indicating that the size of prey in a given chick stage depended on the breeding season (ORLs, $\beta = 0.9$, $z = 8.6$, $d.f. = 1$, $P < 0.0001$). Both terns delivered a higher proportion of tiny prey in 2013 than the rest of the size categories while they delivered a higher proportion of larger prey in the same stage in 2014 (Fig. 1). Similar results were found when the effects of factors were analysed for each species of tern separately (Table 3b, c). For the Cayenne terns,

Table 2 Generalised linear model explaining the variation in the frequency of prey species delivered to their chicks by (a) Royal and Cayenne terns (data from both species pooled), (b) Royal tern and (c) Cayenne tern during the breeding seasons of 2013 and 2014 at Banco Nordeste, Argentina

Explanatory variables	No of parameters	AICc	ΔAIC	*Wi*
(a)				
Sp + BS + CS + CS × BS	5	3594.4	0	0.733
Sp + BS + CS + WS + CS × BS	7	3596.8	2.4	0.218
Sp	2	4054.6	460.2	< 0.001
CS	2	3761.6	167.6	< 0.001
BS	2	4170.1	575.7	< 0.001
WS	3	4175.6	581.2	< 0.001
Null model	1	4172.1	577.7	< 0.001
(b)				
BS + CS + CS × BS	4	4219.6	0	0.552
BS + CS + WS + CS × BS	6	4220.0	0.4	0.448
CS	2	4853.7	634.1	< 0.001
BS	2	4944.7	725.1	< 0.001
WS	2	5229.0	1009.4	< 0.001
Null model	1	5366.1	1146.6	< 0.001
(c)				
BS + CS + CS × BS	4	4706.5	0	0.719
BS + CS + WS + CS × BS	6	4708.4	1.8	0.281
BS	2	5254.4	547.8	< 0.001
CS	2	5533.5	827.0	< 0.001
WS	2	5698.1	991.5	< 0.001
Null model	1	5792.4	1085.8	< 0.001

BS breeding season, *CS* chick stages, *WS* wind speed, *Sp* species

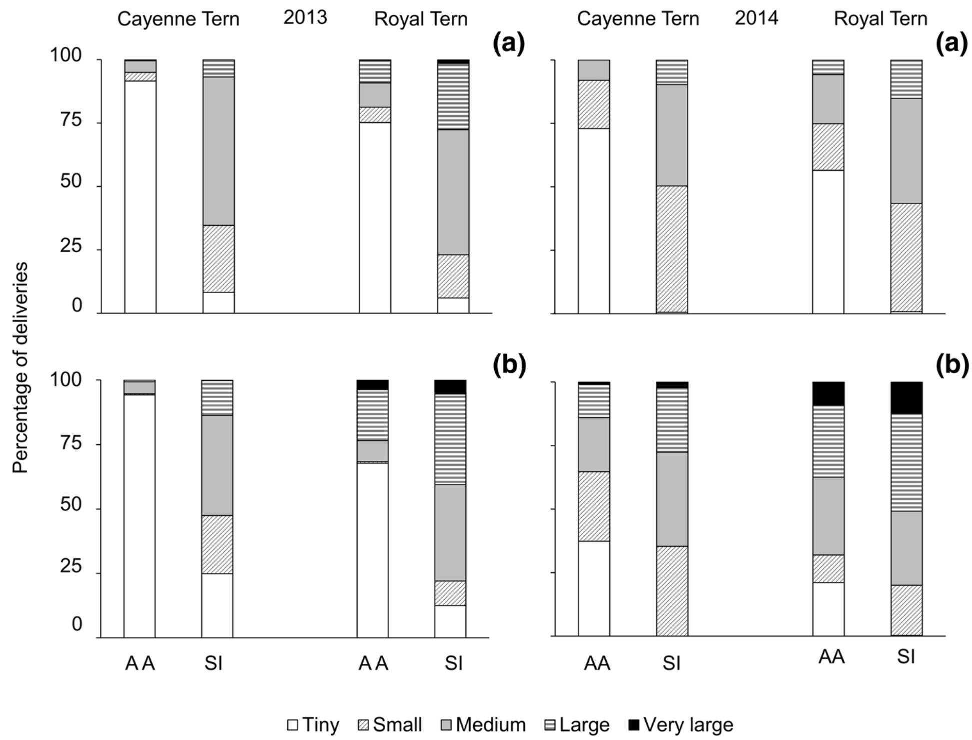

Fig. 1 Frequency of occurrence (%) of sizes of prey delivered to **a** young chicks and **b** old chicks by Royal and Cayenne terns at the Banco Nordeste colony, Argentina, during the 2013 and 2014 breeding seasons. *AA* Argentine Anchovy, *SI* silversides

Table 3 Ordered logistic regressions explaining the variation in the size of prey delivered to their chicks by (a) Royal and Cayenne terns (data from both species pooled), (b) Royal Tern and (c) Cayenne Tern during the breeding seasons of 2013 and 2014 at Banco Nordeste, Argentina

Explanatory variables	No of parameters	AICc	ΔAIC	*Wi*
(a)				
Sp + P + BS + CS + WS + CS × BS	11	16,662.7	0	0.705
Sp + P + BS + CS + CS × BS	9	16,664.4	1.75	0.295
P	5	17,544.1	881.4	< 0.001
BS	5	20,099.3	3436.6	< 0.001
CS	5	20,427.8	3765.1	< 0.001
Sp	5	20,816.0	4390.9	< 0.001
WS	6	20,835.3	4172.6	< 0.001
Null model	1	21,053.6	4390.9	< 0.001
(b)				
P + CS + BS + CS × BS	8	8864.8	0	0.748
BS + CS + WS + CS × BS	10	8867.0	2.2	0.252
P		9148.4	283.6	< 0.001
CS	5	9838.9	974.1	< 0.001
BS	5	10,094.3	1229.5	< 0.001
WS		10,283.0	1418.2	< 0.001
Null model	1	10,387.2	1522.4	< 0.001
(c)				
P + BS + CS + WS + CS × BS	10	7474.6	0	0.976
P + BS + CS + CS × BS	8	7482.0	7.4	0.024
P	5	7806.1	331.5	< 0.001
BS	5	9471.1	1996.5	< 0.001
CS	5	10,063.6	2588.9	< 0.001
WS	6	10,150.6	2675.9	< 0.001
Null model	1	10,283.0	2808.4	< 0.001

P prey, *BS* breeding season, *CS* chick stages, *WS* wind speed, *Sp* species however, the best model included the effect of wind speed, but model parameters indicated that wind speed did not have a significant effect on prey delivery ($P > 0.05$).

Stable isotope analysis

Mean $\delta^{13}C$ values of Royal tern chicks ranged between – 17.4 and – 18.8‰, while $\delta^{15}N$ values ranged between 16.5 and 18.0‰ (Fig. 2a). Mean $\delta^{13}C$ values of Cayenne tern chicks ranged between – 17.6 and – 18.9‰, while $\delta^{15}N$ values ranged between 17.0 and 18.6‰ (Fig. 2a). General mixing polygon sensitivity analysis (using 1500 iterations) showed that isotopic values of all individual samples of both tern species, given the DTDF and prey isotopic values used, were included in more than 95% of the simulated mixing polygons, validating the proposed mixing models (Fig. 2b). Based on the isotopic values corresponding to chicks, the Bayesian mixing model outputs showed that Argentine Anchovy and silversides contributed 35.8 ± 12.6% and 64.2 ± 12.6%, respectively, to Royal Tern diet, and 53.8 ± 12.9% and 46.2 ± 12.9%, respectively, to Cayenne tern diet. No significant differences were found in the consumption of Argentine Anchovy and silversides between the two tern species (Test, $P = 0.443$ and $P = 0.557$, respectively).

No differences were found between species in the isotopic positions of chicks, based on the observed differences in their centroid locations ($P = 0.320$; Fig. 3). The comparison of the isotopic niche width, given by the difference of mean distance to centroid, did not differ significantly from zero ($MDC_{Royal\ tern} - MDC_{Cayenne\ tern} = 0.11$, $P = 0.199$). Furthermore, the absolute value of the difference of nearest-neighbour distances did not differ significantly from zero ($MNN_{Royal\ tern} - MNN_{Cayenne\ tern} = 0.01$, $P = 0.813$). Finally, no significant differences were found in eccentricity values ($ECC_{Royal\ tern} - ECC_{Cayenne\ tern} = 0.15$, $P = 0.725$). Chicks of both species showed a similar spread in their isotopic niche, as no differences were found in their SEA_B (Royal tern: $SEA_B = 1.31$, CI = 1.01–1.52; Cayenne tern: $SEA_B = 1.24$, CI = 0.95–1.43). In accordance with the analysis of centroids, the overlap between the isotopic niches estimated by SEA_C of Royal and Cayenne terns was 65% (Fig. 3).

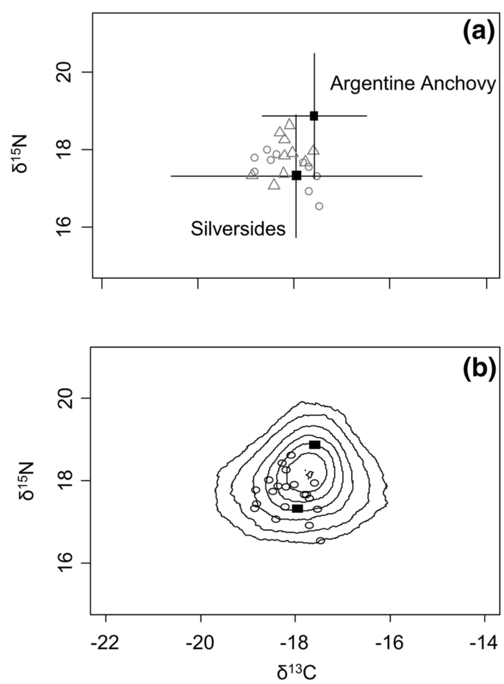

Fig. 2 Dual stable isotope plot of $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) showing the isotopic values of whole blood of Royal and Cayenne tern chicks at Banco Nordeste and their potential prey. **a** Isotopic mixing diagram. Open circles: Royal tern; open triangles: Cayenne tern. Potential prey values corrected for fractionation are represented by solid squares (values are means and error bars ± SD). **b** Simulated mixing region to evaluate the feasibility of the proposed isotopic mixing polygon in Fig. 3a. The positions of individual Royal and Cayenne tern chicks (open circles) and the average source values (solid squares) are shown. Probability contours are at the 5% level (outermost contour) and at every 10% level

Discussion

This study characterizes for the first time the diet of Royal and Cayenne tern chicks at the Bahía San Blas Protected Area, in the northernmost breeding location in Argentine Patagonia. Results of direct observation of prey deliveries indicated that forage fish were a key component in the diet of both species, represented by Argentine Anchovy and multiple species of silversides. Despite distributing observations throughout the chick-rearing stage and encompassing different stages of the tidal cycle and weather conditions,

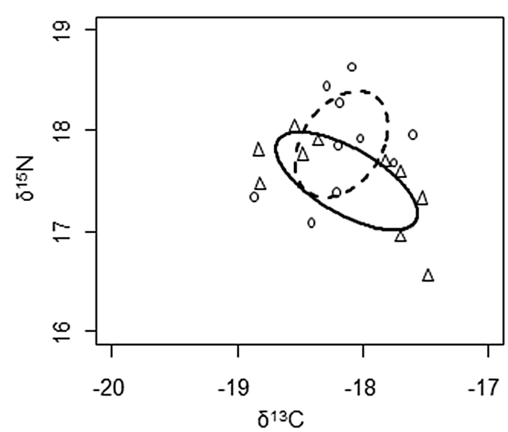

Fig. 3 $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) values for Royal and Cayenne tern chicks at Banco Nordeste during the 2014 breeding season. Isotopic niches are represented as the standard ellipses used to calculate SEA_C. Solid line: Royal tern; dotted line: Cayenne tern. Open circles: Royal tern; open triangles: Cayenne tern

obtaining a representative sample of prey deliveries, direct observations provide detailed information on prey species composition only from the last feeding event (Barrett et al. 2007). However, the key contribution of these forage fish in terms of assimilated biomass throughout the chick growth period was confirmed by stable isotope analysis. Both Royal and Cayenne terns fed their chicks with juvenile fish, particularly in the case of Argentine Anchovy. Results are consistent with those reported for the Punta León colony, 350 kilometres to the south, which indicate that both tern species feed their chick mainly with Argentine Anchovy and the silversides *O. argentinensis* and *O. nigricans* (Quintana and Yorio 1997; Gatto and Yorio 2009).

Partitioning of food resources among syntopically breeding species with similar feeding strategies has been described as a fundamental mechanism to allow species coexistence (Wiens 1989), being frequent in seabirds the partitioning of prey type and size (e.g. Ridoux 1994; Robertson et al. 2014). Royal and Cayenne terns breeding at Punta León showed that diet composition differed between species (Gatto and Yorio 2009). In contrast, although model parameters describing feeding observations at Bahía San Blas indicated some difference in prey composition between tern species, these were quite small. Moreover, both conventional and stable isotope analyses indicated a high overlap in the trophic niche between tern species breeding at Bahía San Blas. Although we lack independent measures of food resources in the study area, diet similarity between both tern species is likely related to high prey availability. Argentine Anchovy is the most abundant pelagic fish in the region and silversides are among the six most abundant species in the Bahía San Blas fish assemblage (Hansen et al. 2001; Llompart 2011). In the Gulf of Mexico, Royal and Sandwich tern chick diet also showed considerable overlap in prey species composition, despite adults of both species partitioned food resources when self-feeding (Liechty et al. 2016). In contrast to the previous study and our results, Royal and Sandwich terns breeding on the east coast of the United States differed in the proportion of prey species fed to their chicks (McGinnis and Emslie 2001). Results obtained in Argentine Patagonia and other regions suggest that segregation in the use of prey by these congeneric terns may be dependent on local food availability and/or composition of fish assemblages, as has been recorded in other seabird species (Barger and Kitaysky 2011).

Although both tern species at Bahía San Blas provided their chicks with similar prey species, Royal terns delivered larger prey than Cayenne terns. These results agree with those reported at the mixed-species colony of Punta León, where the larger Royal tern brought back to the colony larger prey than the Cayenne tern. Similar partitioning of food resources has been observed on the coasts of the United States, where Royal terns delivered larger prey than Sandwich terns (McGinnis and Emslie 2001; Liechty et al. 2016). Segregation by prey size is a common mechanism in breeding assemblages of different-sized seabirds (Fasola et al. 1989; Mancini et al. 2014). Given that seabirds may achieve ecological segregation through a combination of differences in diet, feeding range, and feeding behaviour (Ashmole and Ashmole 1967; Croxall et al. 1997), further studies are needed at Bahía San Blas to adequately assess the partitioning of food resources by these two ecologically similar species.

Prey species delivered to chicks by Royal and Cayenne terns differed between chick stages and breeding seasons, as recorded in several tern species worldwide (McLeay et al. 2009; Ramos et al. 2013). Temporal differences may have resulted from the opportunistic use of different prey species depending on their availability, as anchovies and silversides in the study region experience, like most forage fish, large seasonal and interannual fluctuations (Hansen et al. 2001; Llompart 2011). Prey sizes were smaller in 2013, likely due to the higher frequency of juvenile Argentine Anchovies recorded in tern diet during that year. The reason for the higher abundance of juvenile Argentine Anchovies during 2013 is unclear, as there are no population or behavioural studies on this prey at the needed spatial scale to interpret predator–prey relationships. However, it may reflect the large interannual variation in the timing of egg deposition recorded for this forage fish (Diaz 2010). Royal and Cayenne terns delivered smaller prey during the young chick stage, in agreement with previous studies on these and other tern species that showed an increase in prey size delivered to chick as they grew older (Stienen et al. 2000; Wambach and Emslie 2003; Fernández Ajó et al. 2011; Robertson et al. 2014). Chicks at their early age are expected to be fed with small prey due to their difficulty in manipulating and swallowing large prey (Hulsman 1981; Pereira and Ramos 2009). In addition, prey size is expected to increase as chicks get older, owing to growing energy demands (Ricklefs and White 1981; Shealer 1998).

This study confirms the relevance of forage fish from the Engraulidae and Atherinopsidae families in the trophic ecology of Royal and Cayenne tern populations breeding in the Southwest Atlantic coasts. Given that terns are small, surface-feeding seabirds with relatively small foraging ranges and energetically expensive foraging, they are more vulnerable to food reductions near their breeding colonies (Furness and Tasker 2000). It should be noted that the harvesting of Argentine Anchovy by trawl fisheries shows a marked seasonality, being larger from late winter to late spring (Garciarena and Buratti 2013), when Royal and Cayenne terns start breeding. Silversides are also an important target of recreational fisheries and, in addition, there is interest for the opening in the study area of an artisanal fishery aimed at silversides (Zalba et al. 2008; Llompart 2011). In addition, as

Royal and Cayenne terns prey largely on juvenile forage fish, they may be valuable indicators of fish stocks, as recorded in other tern species (Greenstreet et al. 2009; Velarde et al. 2013). In this context, their trophic requirements should be considered when planning future fisheries development and management in the study area and adjacent waters. However, knowledge on the natural variability, size distribution, and changes in spatial distribution of forage fish are key to correctly assess impacts of fishing forage fish on their predators (Hilborn et al. 2017), and this information is lacking in our study area.

Acknowledgements Thanks to Centro para el Estudio de Sistemas Marinos (CCT CONICET-CENPAT) for institutional support and Dirección de Administración de Áreas Protegidas, Ministerio de Asuntos Agrarios Provincia de Buenos Aires for the permits to conduct the research at the Bahía San Blas protected area. Thanks to N. Bovcon and D. Figueroa for help in the determination of prey species, *O. Frumento* for help in data analysis, and T. Kasinsky for her help in fieldwork.

Funding This study was funded by Wildlife Conservation Society and Consejo Nacional de Investigaciones Científicas y Técnicas (Project PIP no. 112 01 01061).

Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

Ethical approval Animal handling and feather sampling were permitted under appropriate permits (DISPOSICIÓN no 201/12 Dirección de Administración de Áreas Protegidas-Ministerio de Asuntos Agrarios of Buenos Aires Province, Argentina). All applicable international, national, and institutional guidelines for the care and use of animals were followed.

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