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Foraging segregation in tropical and polar seabirds: Testing the Intersexual Competition Hypothesis

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ABSTRACT

The Intersexual Competition Hypothesis (ICH) predicts that sexual size dimorphism (SSD) in seabirds may reduce intraspecific food competition through the exploitation of different trophic niches by each sex. We tested the ICH using stable isotopes (δ^{15}N and δ^{13}C) from whole blood and muscle from six tropical and five polar seabird species sampled at breeding sites. We expected that greater morphological differences between sexes would be related to larger differences in δ^{15}N and δ^{13}C values, reflecting potential diet and spatial segregation between males and females. We also compared trophic segregation in non-tropical and tropical seabirds to determine if there was more intense feeding competition during the generally shorter breeding season in non-tropical areas, leading to more pronounced segregation mechanisms; alternatively, more abundant food resources during breeding at temperate and polar areas, in contrast to oligotrophic tropical areas, could lead to a relaxing of segregation. No significant differences in δ^{15}N or δ^{13}C were found between sexes in seabird species from tropical or polar regions. In addition, there was no correlation between total dimorphism index and differences in mean δ^{15}N or δ^{13}C values of females and males for each species. Analysis of data from the literature, accounting for phylogeny, indicated that size-dimorphic seabird species from temperate and polar regions tend to show trophic (δ^{15}N) or spatial (δ^{13}C) segregation (71%; 30 out of 42 study cases) more often than tropical dimorphic species (19%; 3 out of 16 study cases). Overall, SSD seems to facilitate trophic or spatial segregation in non-tropical seabirds, but not in tropical species. Further investigations are necessary to confirm the lack of this pattern in tropical seabirds.

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1. Introduction

Sexual size dimorphism (SSD), where one sex is larger than the other, has been reported for many taxa, including seabirds (Fairbairn and Shine, 1993; Fairbairn et al., 2007; Shine, 1989). Many hypotheses explain SSD as the result of sexual selection or niche segregation (Andersson and Norberg, 1981; Krüger, 2005; Shine, 1989). Sexual size dimorphism may also be related to the different parental roles of each sex — larger females can store more energy for reproduction and produce larger broods or chicks, care for more young or better defend territories (Andersson, 1994; Shine, 1989; Weimerskirch et al., 2009). Conversely, male-biased SSD is expected to result from sexual selection, as males' larger size gives them advantages in intra-sexual contests for mates and in attracting females (Andersson, 1994) or territory defense (Nelson, 2005). The Intersexual Competition Hypothesis (ICH) predicts that SSD in birds may reduce intraspecific food competition, as males and females exploit different trophic or dietary niches (Selander, 1966). In addition, this hypothesis predicts that differences in morphology (e.g., body size) results in the segregation of males and females in relation to diet composition (Awkerman et al., 2007; Forero et al., 2002, 2005; González-Solís and Croxall, 2005; Selander, 1966). Such segregation may also be spatial, where males and females exploit different foraging areas or depths (Cook et al., 2013; González-Solís and Croxall, 2005; Weimerskirch et al., 1993, 2006) or at different time of the day (Paredes et al., 2008). The ICH can be tested using colonial nesting seabirds where there is a high density of individuals competing for limited prey resources, and they are constrained by their nest-bound chick to central-place foraging, which limits adult foraging behavior (Ainley et al., 2004; Forero et al., 2002). Seabirds represent a variety of points along the SSD continuum and show varying degrees of dietary segregation (González-Solís et al., 2000; Stauss et al., 2012;

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Weimerskirch et al., 2009). Furthermore, Phillips et al. (2011) hypothesized that the extent of sexual segregation in foraging ecology was a function of sexual size dimorphism, which varies considerably among species.

Trophic niche segregation is often assessed using differences in diet, and it is the most frequently studied component of ecological niche segregation, but there are limitations associated with conventional dietary analysis (Barrett et al., 2007; Bearhop et al., 2004). Traditionally, quantifying trophic segregation has been based on analysis of stomach contents, pellets or regurgitations (Barrett et al., 2007; Duffy and Jackson, 1986; Karnovsky et al., 2012). However, these methods reflect only the most recent food consumed, and prey species differ in their digestion rates, which affects estimates of diet composition. Attached position-logging devices have increased our ability to track birds and quantify their spatial niche (Wilson and Vandenabeele, 2012; Wilson et al., 2002), but such methods are usually expensive and are not feasible for tracking movements of smaller species (Hobson, 1999; Wikelski et al., 2007). Stable-nitrogen and carbon isotopes have been applied extensively in the past two decades to understand trophic niche segregation (Bearhop et al., 2002; Hobson, 2011; Hobson et al., 1994). Isotope values in seabird tissue are derived from the values of their prey and may indicate the origin and type of prey consumed (Hobson and Clark, 1992; Kelly, 2000). The stable-carbon isotope ratio ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) is higher in inshore as compared to offshore feeding animals (Cherel et al., 2008; Hobson and Welch, 1992; Hobson et al., 1994), making it a useful tool for the study of spatial segregation in foraging areas. On the other hand, stable-nitrogen isotope values ($^{15}N/^{14}N$, or $\delta^{15}N$) increase with trophic position in a stepwise manner (Post, 2002). Using stable isotopes to investigate trophic niches is facilitated by the large variety of isotopic values within and among food webs (Newsome et al., 2007). The isotopic niche can be represented as an area in 2-dimensional space with isotopic values as coordinates, where axes represent relative proportions of isotopically distinct resources incorporated into an animal's tissues (Bearhop et al., 2004; Newsome et al., 2007).

Tropical seabirds live in an oceanic environment with lower productivity and less seasonality where prey are distributed more erratically than in temperate and polar oceans (Ballance et al., 1997; Longhurst and Pauly, 1987). Most tropical seabirds must travel extensively to their feeding ground, where they feed mainly on fish and squid within the first few meters of the water column, by aerial feeding and plunge diving (Ashmole and Ashmole, 1967; Diamond, 1983; Harrison et al., 1983; Nelson, 2005; Weimerskirch et al., 2006). Non-tropical (i.e., polar and temperate) seabirds include more species that can exploit the ocean through pursuit dives, including planktivores, piscivores, squid-eaters and apex predator-scavengers (Ainley and Boekelheide, 1983; Hobson et al., 1994; Ridoux, 1994; Sydeman et al., 1997). However, tropical seabirds feed on a broad variety of prey and frequently diet diversity is much greater than for non-tropical species (Harrison et al., 1983). These differences in seabird foraging ecology are related to the differences in productivity of the world's oceans (Ballance and Pitman, 1999). Examining the ICH in seabirds from tropical and polar areas can be used for both seabird management and fisheries management.

In this study we tested the ICH using 11 seabird species from tropical and Arctic breeding sites and hypothesized that size-dimorphic species would show greater trophic segregation than monomorphic species. Specifically, we expected that greater morphological differences between sexes would be related to greater differences in tissue $\delta^{15}N$ and $\delta^{13}C$ values, reflecting trophic segregation between males and females. We also compared trophic segregation between tropical and non-tropical seabirds to determine if differences in trophic segregation were potentially due to more intense feeding competition during the shorter breeding season in non-tropical areas, leading to more pronounced segregation mechanisms; alternatively, more abundant food resources during breeding in non-tropical areas, in contrast to oligotrophic tropical areas, could lead to a relaxing of segregation. In order to study the intraspecific trophic segregation in tropical and non-tropical seabirds, our objectives were: 1. to classify the degree of dimorphism between sexes using a dimorphism index, based on morphological characteristics; 2. to identify trophic and spatial segregation between males and females of each species using stable isotope analysis; and 3. to perform a literature review to determine if dimorphism and trophic segregation were more common in non-tropical than in tropical seabirds.

2. Materials and methods

2.1. Study sites and species

We analyzed data from tropical and polar systems that were collected as part of two larger studies conducted in the Canadian Arctic (Hobson and Bond, 2012; Hobson et al., 2002 and on tropical Brazilian islands (Mancini et al., in press). We studied five species in the Northwater Polynya (between 75°84′N, 78°82′W and 77°140′N, 69°100′W): Black guillemot (*Cepphus grylle*), Black-legged kittiwake (*Rissa tridactyla*), Dovekie (*Alle alle*), Northern fulmar (*Fulmarus glacialis*) and Thick-billed murre (*Uria lomvia*); and six species in Brazil: Brown booby (*Sula leucogaster*), Masked booby (*Sula dactylatra*), Brown noddy (*Anous stolidus*), Black noddy (*Anous minutus*), Sooty tern (*Onychoprion fuscatus*) and Red-billed tropicbird (*Phaethon aethereus*; Table 1). The seabird species from Brazil were from four sites: archipelagos of Fernando de Noronha (03°51′S, 32°25′W), Abrolhos (17°20′S, 38°35′W), São Pedro and São Paulo (00°55′N, 29°20′W; SPSPA) and Atol das Rocas (3°51′S, 33°49′W). Furthermore, we conducted a literature review to gather studies that used stable isotopes analysis to investigate sex-related trophic and spatial segregation in seabirds from tropical and non-tropical areas.

2.2. Sampling methods

Tropical seabirds were captured with dip net or by hand, and weighed them using a digital balance or dynamometer (±5 g). Measurements of culmen and tarsus length were taken with the use of callipers (±0.1 mm) and wing length with a stopped wing ruler (±1 mm). Samples were collected from SPSPA in August 2010, from Atol das Rocas in September/October 2010, from Fernando de Noronha in March and July 2011, and from Abrolhos in February and August 2011. Blood from the tarsal vein was collected with syringe and needle from adults and a drop was placed on FTA cards for sex determination of tern, noddy and tropicbird species using the CHD genes (Fridolfsson and Ellegren, 1999). In boobies, sex was determined by vocalization, or colors of the head skin and bill. Polar seabirds from the Northwater Polynya were collected at sea by shooting (under a permit from the Canadian Wildlife Service) from May to July 1998, and August to September 1999, for other studies (Hobson and Bond, 2012; Hobson et al., 2002). They were sexed by dissection after tissue sampling. Birds were weighed using a digital balance (to the nearest 1 g or 5 g), culmen length was measured using callipers (±0.1 mm), and wing length was measured using a stopped wing ruler (±1 mm).

For stable isotope analysis from tropical seabirds, we collected whole blood (~0.5 ml) from the tarsal vein with syringe and needle from adults and placed on glass slides, air dried, transferred and stored in labeled vials until analysis. Muscles were collected from polar seabirds, which represent the whole breeding period (Hobson and Bond, 2012), and lipids were removed using a 2:1 chloroform:methanol solution. Muscle and blood samples were freeze-dried, ground and homogenized. Subsamples of 1 mg were weighed into tin cups for analysis of $\delta^{13}C$ and $\delta^{15}N$.

2.3. Stable-isotope analysis

For tropical seabirds, samples were analyzed in two laboratories: Laboratory of Analytical Chemistry at University of Georgia (USA) and

Table 1
Dimorphism index (DI) of seabird species from tropical and polar regions.

Species	Scientific name	Site	DI c	DI cub.m	DI t	DI w	ΣDI	SSD	Dif N	Dif C	P
Brown noddy	*Anous stolidus*	AT	0.00	0.02	0.01	0.01	0.04	M	0.1	0.0	0.709
Red-billed tropicbird	*Phaethon aethereus*	AB	0.03	0.01	0.00	0.01	0.05	D	0.3	0.1	0.366
Thick-billed murre	*Uria lomvia*	NOW	0.03	0.01	0.00	0.02	0.06	M	0.0	0.0	0.251
Black guillemot	*Cepphus grylle*	NOW	0.04	0.00	0.03	0.01	0.08	M	0.0	0.0	0.355
Masked booby	*Sula dactylatra*	AB	0.01	0.03	0.03	0.01	0.08	D	0.7	0.4	0.003
Sooty tern	*Onychoprion fuscatus*	AT	0.03	0.02	0.02	0.01	0.08	D	0.2	0.1	0.044
Black noddy	*Anous minutus*	SPSPA	0.03	0.03	0.00	0.02	0.08	M	0.0	0.3	0.132
Brown noddy	*Anous stolidus*	AB	0.01	0.00	0.04	0.03	0.08	M	0.0	0.1	0.062
Brown booby	*Sula leucogaster*	SPSPA	0.01	0.06	0.00	0.02	0.09	D	0.2	0.0	0.002
Dovekie	*Alle alle*	NOW	0.05	0.01	0.02	0.02	0.10	D	0.0	0.0	0.000
Black noddy	*Anous minutus*	FN	0.04	0.04	0.03	0.01	0.12	M	0.3	0.2	0.097
Masked booby	*Sula dactylatra*	FN	0.02	0.04	0.06	0.02	0.14	D	0.5	0.0	0.000
Brown noddy	*Anous stolidus*	SPSPA	0.02	0.05	0.06	0.03	0.16	D	0.1	0.0	0.000
Masked booby	*Sula dactylatra*	AT	0.04	0.05	0.04	0.03	0.16	D	0.1	0.1	0.001
Black-legged kittiwake	*Rissa tridactyla*	NOW	0.07	0.03	0.05	0.02	0.17	D	0.0	0.0	0.000
Brown booby	*Sula leucogaster*	AB	0.03	0.07	0.05	0.04	0.19	D	0.3	0.3	0.000
Brown booby	*Sula leucogaster*	FN	0.04	0.07	0.04	0.04	0.19	D	0.0	0.1	0.000
Brown booby	*Sula leucogaster*	AT	0.04	0.06	0.07	0.04	0.21	D	0.0	0.3	0.000
Northern fulmar	*Fulmarus glacialis*	NOW	0.08	0.04	0.07	0.07	0.26	D	0.0	0.0	0.001

NOW = Northwater Polynya, AT = Atol das Rocas, AB = Abrolhos, FN = Fernando de Noronha, SPSPA = São Pedro and São Paulo Archipelago, c = culmen, cub.m = cube root of body mass, t = tarsus, w = wing, SSD = sexual size dimorphism, M = monomorphic, D = dimorphic, Dif N or C = difference in δ^{15}N or δ^{13}C between sexes.

Stable Isotope Hydrology and Ecology Research Laboratory (Canada). Two laboratory standards were analyzed for every 12 unknown samples. Stable isotope values are expressed in δ-notation as parts per thousand (‰) differences from the international reference material Vienna Pee Dee Belemnite limestone (carbon) and air (nitrogen). Measurement precision of both δ^{15}N and δ^{13}C measurements was <0.2‰ in both laboratories. We tested for any systematic differences among laboratories (Mill et al., 2008) by comparing replicate analyses of homogenized δ^{15}N and δ^{13}C values of growing feathers (N = 10) of Yellow-nosed albatross (*Thalassarche chlororhynchos*). A paired-*t* test showed no significant difference between the results obtained (δ^{15}N: $t = 2.08$, $P = 0.07$; δ^{13}C: $t = 0.56$, $P = 0.59$), indicating that values obtained in the two laboratories could be pooled together. Analytical methods for samples from polar seabirds are detailed by Hobson et al. (2002) and Hobson and Bond (2012).

2.4. Statistical analysis

Seabird species were classified as dimorphic or monomorphic by analyzing all measurements together (culmen, tarsus, wing length and cubed root of body mass) using a PERMANOVA analysis (permutational multivariate ANOVA, Anderson et al., 2008). Species with statistically significant morphometric differences ($P < 0.05$) were classified as dimorphic, and those with $P > 0.05$ classified as monomorphic. We used the cube-root of body mass, since linear measurements scale to body mass$^{1/3}$ (Fairbairn et al., 2007). In order to quantify dimorphism differences on a continuous scale, we calculated the mean culmen, wing, and tarsus length, and cube root of body mass for each sex and species, and determined the dimorphism index (DI) for all measurements following Gibbons and Lovich (1990) as: (larger sex/smaller sex) − 1. We then summed the DI values ($DI_{culmen} + DI_{tarsus} + DI_{wing} + DI_{cube\ root\ body\ mass}$ = total DI) for each species, which represent the total dimorphism index (total DI). We then used the mean δ^{13}C and δ^{15}N values for each sex to calculate the degree of intersexual trophic or spatial segregation for each species (e.g., $\delta^{13}C_{large\ sex} - \delta^{13}C_{small\ sex}$). We used a Pearson correlation with Student's *t*-test between the total DIs of each species and the difference in mean δ^{13}C and δ^{15}N values to test whether trophic segregation was related to size dimorphism in tropical and polar systems. We used a two-tailed Student's *t*-test to determine if the sexes were isotopically segregated for each species and site. We employed the false discovery rate (FDR) procedure (Benjamini and Hochberg, 1995) to adjust P-values for multiple comparisons. To compare the variances between total DI in monomorphic and dimorphic species we applied Student's *t*-test, because data were homoscedastic and normally distributed (Zar, 2010).

Finally, we reviewed the literature for studies testing differences between sexes in δ^{13}C and δ^{15}N values during the breeding season to quantify the percentage of monomorphic and dimorphic seabird species that showed isotopic segregation. Isotopic segregation in δ^{13}C or δ^{15}N values and classification of species as monomorphic or dimorphic were determined from the original source/paper (Appendix 1).

We built 1000 phylogenetic trees to determine if there was a phylogenetic effect in the analysis from the literature review. We used the website http://birdtree.org/ (Jetz et al., 2012), based on the phylogenetic hypothesis proposed by Ericson et al. (2006) as a 'backbone'. A strict consensus tree was then built in Mesquite 2.75 (Maddison and Maddison, 2010) for use in subsequent analyses. Then we measured the phylogenetic signal of binary traits using D statistic proposed by Fritz and Purvis (2010). The binary traits were: niche segregation between sexes (yes or no), SSD (monomorphic or dimorphic), and regions (tropical or non-tropical). D is based on the sum of the differences in the state of the respective trait (0 or 1) for sister clades across the phylogeny. The sum of sister-clade differences will be lowest for strongly clumped traits and highest for strongly overdispersed ones (Fritz and Purvis, 2010). D = 1 if the distribution of the binary trait is random with respect to phylogeny, D = 0 if the binary trait is distributed as expected under the Brownian motion model of evolution, and D < 0 if the binary trait is more phylogenetically conserved than the Brownian expectation (Fritz and Purvis, 2010).

We used a 2×2 χ^2 test, with Yates correction, for non-tropical seabird studies, in order to test if dimorphic and monomorphic species differed in relation to trophic segregation. For tropical seabirds, as the number of studies in each category (monomorphic vs. dimorphic; segregated vs. non-segregated) included zero and values <5, we applied Fischer's Exact test (Zar, 2010).

3. Results

3.1. Dimorphic and monomorphic species

Both Brown and Masked boobies showed sex differences in size with the combined four measurements analyzed, in four tropical islands. SSD was also found in Brown noddy from SPSPA, Red-billed tropicbird and Sooty tern (Table 1). For polar seabirds the four combined measurements differed between sexes in the Northern fulmar, Dovekie and Black-legged kittiwake (Table 1). All these species were considered

dimorphic, while the others were considered monomorphic: Black guillemot, Thick-billed murre, Black noddy and Brown noddy from Atol das Rocas and Abrolhos. In tropical and polar seabirds total DI varied more in dimorphic than in monomorphic species (Student's *t*-test, $t_{17} = 2.57$, P = 0.019, Table 1).

3.2. Isotopic segregation between sexes in seabirds from Northwater Polynya and Brazilian waters

No significant differences in δ^{15}N or δ^{13}C were found between sexes in any seabird species after the FDR procedure for tropical or polar regions (Table 2). Regressions using the differences in mean values of each isotope (δ^{15}N and δ^{13}C) between sexes for each species and their respective total DIs did not show any significant values for polar (δ^{15}N vs. DI: $t_3 = 0.36$, P = 0.74; δ^{13}C vs. DI: $t_3 = 0.49$, P = 0.66) and tropical seabirds (δ^{15}N vs. DI: $t_{12} = -0.74$, P = 0.48; δ^{13}C vs. DI: $t_{12} = 0.47$, P = 0.64, Fig. 1).

3.3. Literature review

Thirty-seven studies, including Hobson and Bond (2012) and Mancini et al. (in press), quantified intersexual foraging differences in trophic level (δ^{15}N) and/or spatially (δ^{13}C) in 49 seabird species. Thirty-seven species were from polar and temperate areas and 12 from tropical areas (Appendix 1). In the reviewed papers, dimorphic species in non-tropical areas showed significant differences in δ^{15}N or δ^{13}C values between sexes in 71% (30 out of 42) of cases, while in the tropics this value was 19% (3 out of 16). Differences in only δ^{13}C values between sexes were found for Waved albatross (*Phoebastria irrorata*) in the tropics and in seven species in non-tropical areas (marked in Appendix 1), of which only Audouin's gull (*Ichthyaetus audouinii*) was categorized as monomorphic. In the tropics, Brown and Red-footed (*Sula sula*) boobies showed either no trophic or spatial segregation or only isotopic spatial segregation (one study each), as did Wandering albatross (*Diomedea exulans*) in South Georgia and Scopoli's shearwater (*Calonectris diomedea*) (Appendix 1). Otherwise, in non-tropical and tropical seabirds, 65% (11 out of 17) and 100% (2 out of 2) of monomorphic species did not show isotopic differences between sexes, respectively (Appendix 1). No phylogenetic signal was found for SSD (D = 0.62) or niche differences (D = 0.76). The probabilities of D values being generated by Brownian model evolution (BM) or being not phylogenetically structured (NP) are respectively 0.06 and 0.08 for SSD and 0.02 and 0.17 for niche differences. Nonetheless, the binary trait for region showed phylogenetic signal (D = −0.34) and their probabilities were BM = 0.75, NP < 0.001. There were significant differences in trophic segregation between dimorphic and monomorphic species in non-tropical regions ($\chi^2 = 6.64$, df = 1, P = 0.02), but this was not detected in tropical seabirds (Fisher's Exact test, P = 0.67).

4. Discussion

4.1. Sexual size dimorphism and trophic segregation

Our data from Northwater Polynya and Brazil did not support the Intersexual Competition Hypothesis for tropical and polar seabird species. This hypothesis predicts that differences in body size between sexes

Table 2
Stable isotopes results for polar and tropical seabird species, with false discovery rate correction (FDR).

Site	Species	Sex	N	δ^{15}N	*t*	P	FDR	δ^{13}C	*t*	P	FDR
Abrolhos	MB	F	11	9.5 ± 0.7	1.691	0.113	0.016	−16.3 ± 0.3	−2.737	0.016	0.003
		M	11	9.9 ± 0.9				−16.7 ± 0.2			
	RBT	F	4	8.9 ± 0.6	0.775	0.454	0.037	−16.9 ± 0.2	0.692	0.503	0.026
		M	9	8.6 ± 0.5				−17.0 ± 0.2			
	BB	F	7	11.0 ± 0.7	−0.881	0.393	0.032	−16.3 ± 0.4	−1.797	0.093	0.011
		M	8	10.7 ± 0.9				−16.6 ± 0.3			
	BN	F	9	10.5 ± 0.1	−0.034	0.973	0.050	−18.6 ± 0.2	0.992	0.337	0.021
		M	7	10.5 ± 0.1				−18.5 ± 0.2			
Atol das Rocas	ST	F	10	9.5 ± 0.3	0.985	0.338	0.029	−18.2 ± 0.1	0.974	0.343	0.024
		M	10	9.7 ± 0.2				−18.1 ± 0.3			
	BN	F	9	9.3 ± 0.1	1.002	0.329	0.026	−17.9 ± 0.2	−0.303	0.765	0.047
		M	11	9.4 ± 0.2				−17.9 ± 0.2			
	MB	F	10	10.1 ± 0.1	−1.315	0.205	0.024	−16.6 ± 0.2	0.562	0.584	0.032
		M	10	9.9 ± 0.2				−16.5 ± 0.1			
	BB	F	9	10.0 ± 0.3	0.122	0.904	0.047	−16.7 ± 0.3	−1.976	0.066	0.008
		M	9	10.0 ± 0.3				−16.9 ± 0.3			
F. de Noronha	BLN	F	4	7.8 ± 0.3	1.305	0.193	0.021	−17.5 ± 0.1	1.305	0.212	0.016
		M	10	8.1 ± 0.5				−17.3 ± 0.2			
	MB	F	9	10.7 ± 0.4	−3.343	0.003	0.003	−16.3 ± 0.3	−0.03	0.764	0.045
		M	9	10.4 ± 0.2				−16.3 ± 0.1			
	BB	F	9	9.9 ± 0.1	0.481	0.636	0.045	−16.5 ± 0.3	−0.427	0.675	0.042
		M	8	9.9 ± 0.2				−16.6 ± 0.2			
SPSPA	BN	F	8	9.2 ± 0.2	−1.413	0.176	0.018	−17.8 ± 0.1	−0.187	0.853	0.050
		M	9	9.3 ± 0.2				−17.9 ± 0.3			
	BLN	F	6	8.9 ± 0.2	0.487	0.632	0.042	−18.2 ± 0.5	1.216	0.239	0.018
		M	5	8.9 ± 0.3				−18.5 ± 0.6			
	BB	F	10	10.5 ± 0.2	−2.168	0.044	0.011	−16.9 ± 0.2	0.462	0.661	0.039
		M	10	10.3 ± 0.2				−16.9 ± 0.1			
Northwater Polynya	DO	F	61	11.3 ± 0.6	−0.855	0.394	0.034	−20.4 ± 0.6	−0.560	0.577	0.029
		M	51	11.4 ± 0.5				−20.3 ± 0.5			
	BG	F	14	14.5 ± 0.8	−1.661	0.109	0.013	−20.1 ± 0.7	2.170	0.040	0.005
		M	14	15.0 ± 0.7				−20.5 ± 0.5			
	NF	F	9	13.8 ± 0.5	−2.274	0.037	0.008	−20.2 ± 0.7	−0.515	0.614	0.034
		M	9	14.4 ± 0.5				−20.0 ± 0.8			
	BLK	F	14	13.7 ± 0.6	−0.583	0.566	0.039	−20.4 ± 0.7	−1.421	0.172	0.013
		M	9	13.8 ± 0.9				−20.0 ± 0.8			
	TBM	F	19	14.2 ± 0.6	−2.326	0.026	0.005	−20.3 ± 0.6	−0.473	0.638	0.037
		M	37	13.8 ± 0.7				−20.2 ± 0.5			

FDR > P should be considered significant. F = female, M = male, MB = Masked booby, RBT = Red-billed tropicbird, BB = Brown booby, ST = Sooty tern, BN = Brown noddy, BLN = Black noddy, DO = Dovekie, BG = Black guillemot, NF = Northern fulmar, BLK = Black-legged kittiwake, TBM = Thick-billed murre. Scientific names are given in Table 1.

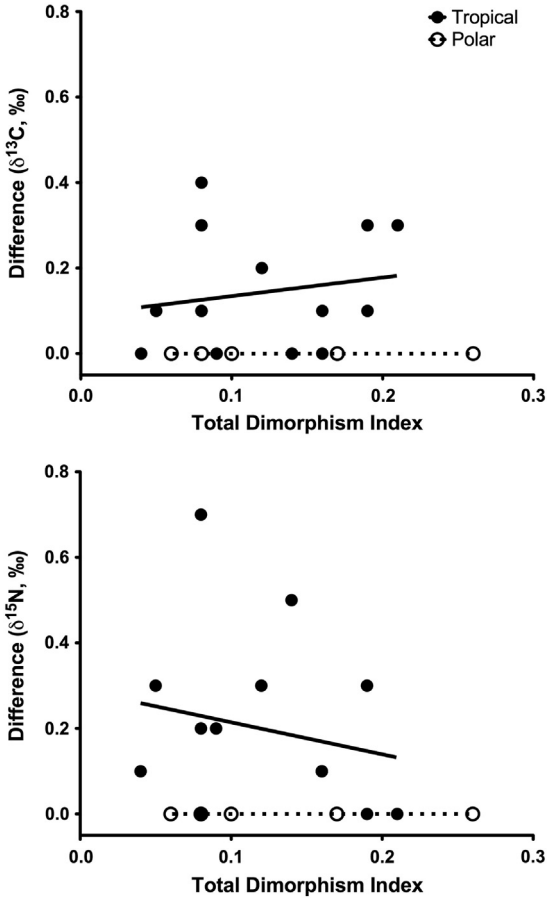

Fig. 1. Total dimorphism index and the stable isotopes differences (δ^{15}N and δ^{13}C) between sexes, in tropical and polar seabird species during the breeding season. No significant trend was found. Dashed lines refer to polar seabird trend, while black lines refer to tropical seabird trend.

have evolved through trophic niche segregation to enable more efficient intraspecific foraging, and greater reproductive success (González-Solís et al., 2000), and such segregation is common during the breeding season (Phillips et al., 2011). This segregation may happen due to constrained foraging closer to breeding colonies where competition between sexes is greater, as seabirds are central-place foragers. Thus, morphological differences could lead males and females to explore different trophic niches, differing in their prey species or foraging areas (Cook et al., 2013; Navarro et al., 2009; Ramos et al., 2009). The larger sex generally has access to a larger range of prey sizes and trophic levels (Awkerman et al., 2007; Bearhop et al., 2006), increasing variation in diet composition compared to the smaller sex. In birds, the average size difference between the sexes is 5%–10% (Amadon, 1959). In our study, tropical species with more accentuated dimorphism had total dimorphism index varying from 8% to 16% in Masked boobies and 9% to 21% in Brown boobies. In dimorphic polar seabirds this index ranged from 11% in Dovekies to 26% in Northern fulmars. Though total dimorphism index includes the cube root of body mass, body mass may be more variable within the breeding season (Croxall, 1995), but it is an important character in niche segregation because heavier birds may dive deeper, or forage in different areas, as documented for sulids (boobies and gannets; Lewis et al., 2002; Weimerskirch et al., 2006, 2009), penguins (Forero et al., 2002), albatrosses and petrels (Forero et al., 2005; Phillips et al., 2004; Weimerskirch et al., 1993).

Phillips et al. (2011) hypothesized that the degree of dimorphism was proportional to the degree of trophic segregation. However, contrary to this, and our expectations, we found no significant correlation between the degree of sexual dimorphism and the trophic differences between sexes in either tropical or polar seabirds during the breeding season. Trophic segregation depends on prey availability and abundance, and in order to identify this segregation between sexes using stable isotopes, the prey must differ isotopically. When seabirds feed on the same prey, there is high overlap in stable isotope values (Bugoni et al., 2010; Catry et al., 2008). Even for markedly dimorphic species, such as boobies, Black-legged kittiwakes and Northern fulmars, there was no trophic segregation between sexes. Nevertheless, the lack of differences in stable isotope values should be interpreted with caution and does not necessarily mean that birds from both sexes were feeding on the same resources or were not spatially segregated. The species could be feeding on different prey with similar δ^{15}N values (Bearhop et al., 2004; Forero et al., 2002; Lavoie et al., 2012) or in different areas, but with homogeneous δ^{13}C values (Graham et al., 2010; McMahon et al., 2013; Weimerskirch et al., 2009), or even at different depths, but without distinct δ^{13}C values (Weimerskirch et al., 2009). In such cases, males and females could show overlapping isotopic niches, but still have distinct trophic or spatial niches. On the other hand, stable isotope analysis has many advantages over more traditional methods. This method of measuring foraging is more prone to show intraspecific differences than conventional ones, because stable isotope analysis integrates diet information over time and space (Hobson et al., 1994). However, conventional dietary studies can complement stable isotopes analysis with more detailed dietary information (Bearhop et al., 2001; Hedd and Montevecchi, 2006).

4.2. Literature review — non-tropical and tropical seabirds

In general, polar and temperate seabirds have a shorter time available for breeding each year than tropical species, due to the constraints imposed on them by a seasonal climate. They need to cope with lower temperatures and a breeding period that approaches the maximum available time (Schreiber and Burger, 2002). This small 'breeding window' could stimulate trophic segregation between males and females and enhance their SSD, leading the two sexes to explore different foraging grounds or prey, reducing competition.

In non-tropical regions, the majority of seabird populations depart from a colony in specific directions, implying that prey availability is predictable in both time and space (Weimerskirch, 2007). Prey is seasonally abundant during the seabird breeding season, e.g., krill (*Euphausia superba*) in Antarctica, Argentine anchovy (*Engraulis anchoita*) in Patagonia (Forero et al., 2002, 2004), Arctic cod (*Boreogadus saida*) in the Arctic (Hobson and Welch, 1992) and capelin (*Mallotus villosus*) in Newfoundland and Labrador (Carscadden et al., 2002). In addition, differences in prey and foraging areas may be explained by dietary specialization between sexes (Forero et al., 2005; Phillips et al., 2011) or a differential role of the sexes in parental care (Harding et al., 2008). Sex differences in diet may also occur in colonies with diverse oceanographic conditions and prey availability (e.g., the size of chick meals delivered by Dovekies differed between male and female parents in one study, but were similar in another study under different environmental conditions; Roby et al., 1981; Wojczulanis et al., 2006). Feeding in association with oceanographic features such as marine fronts and mesoscale eddies, is important for non-tropical seabirds (Acha et al., 2004; Hyrenbach et al., 2006; Russell et al., 1999), but its significance in the tropics remains poorly known (Ballance et al., 1997, 2006).

Seabirds breeding in tropical and subtropical areas are less confined to a season by weather conditions, but food availability is still generally unpredictable and prey species are distributed patchily (Longhurst and Pauly, 1987; Weimerskirch, 2007). Tropical seabirds are constrained to feed near or above the water surface. In contrast, non-tropical seabirds exhibit a wider spectrum regarding foraging depth (e.g., obligate surface feeders as gadfly petrels, storm-petrels and terns, to deep diving species such as penguins, auks and cormorants; Ballance and Pitman, 1999). Furthermore, most tropical species forage in association with subsurface

predators that drive food to the surface, increasing the erratic nature of food resources (Ballance and Pitman, 1999; Ballance et al., 1997), though these feeding opportunities have been suggested as important for some non-tropical species as well (Grebmeir and Harrison, 1992; Obst and Hunt, 1990).

Trophic segregation between sexes in dimorphic tropical seabirds was reported only in Waved albatross (Awkerman et al., 2007), Red-footed booby (Cherel et al., 2008), and Brown booby (Young et al., 2010a). However, two other studies, for the latter two species, did not find evidence of intersexual foraging or trophic differences (Weimerskirch et al., 2009; Young et al., 2010b; this study). Furthermore, Waved albatross breed at the Galapagos Archipelago, which has sea-surface temperatures (SST) similar to temperate areas (SST <23 °C; Ballance and Pitman, 1999), and the oceanographic features in that region could contribute to niche segregation in this species, despite not being reported for Blue-footed booby (*Sula nebouxii*) at the same place (Cruz et al., 2012). Therefore, in the tropics, it is possible that size dimorphism could be more related to sexual selection, or selection associated with differences in reproductive roles, and not partitioning of feeding resources. Resources may also vary in space and time, resulting in low selection for different feeding methods, isotopically different prey, and morphologies associated with them.

Seabirds are central place foragers during the breeding season (Masello et al., 2010), and areas close to breeding colonies can be isotopically homogeneous, making it difficult to find isotopic differences among foraging areas. For example, in Brown and Blue-footed boobies from the Gulf of California, females foraged farther from the colony than males (on average 50 and 30 km farther, respectively), but there were no differences in δ^{13}C values between sexes (Weimerskirch et al., 2009). These authors suggested that there was no linear relationship between morphology and its effect, because the differences in body mass and size between males and females were similar for both species, but the differences in foraging behavior between sexes were more noteworthy for Brown- than for Blue-footed booby. Trophic segregation has also been reported for several monomorphic species such as Northern gannets (*Morus bassanus*, Lewis et al., 2002), Common terns (*Sterna hirundo*, Nisbet et al., 2002) and Thin-billed prions (*Pachyptila belcheri*, Quillfeldt et al., 2008). This suggests that differences in foraging between sexes may arise independent of sexual dimorphism in body size, but probably due to competition for resources. Moreover, physiological conditions might also differ between sexes (Owen et al., 2005), affecting its isotopic values and potentially obscuring or biasing differences that are often assumed to reflect only diet or foraging location (Ehrich et al., 2010; Wolf et al., 2009). This may happen particularly in species with SSD where the larger sex has higher energy requirements (Magrath et al., 2007).

Finally, we must consider the number of studies that examined trophic segregation using stable isotopes. In our literature review, 82% (N = 38) of the studies used stable isotopes to investigate sexual trophic segregation (or the absence thereof) in polar and temperate seabirds. Therefore, the total number of dimorphic species showing trophic segregation in non-tropical regions could be biased by the greater number of studies outside the tropics. There was a phylogenetic signal for region, which means that species were grouped according to areas, but there is no phylogenetic trend in relation to SSD and niche differences. That is to say that although the bird fauna occurring in different regions belonged to distinct clades, such geographic differentiation in phylogenetic distribution of species did not result in ecological differentiation. Moreover, additional studies with tropical seabirds may support the trends highlighted in this paper.

5. Conclusions

We did not find differences in stable isotope values between sexes, or a correlation between the degree of isotopic trophic segregation and the degree of SSD in tropical or polar seabird communities, contrary to the expectation based on the Intersexual Competition Hypothesis. However, our literature review indicated that dimorphic seabird species from polar/temperate regions are more prone to show trophic or spatial segregation than dimorphic species from the tropics. Therefore, sexually dimorphic seabirds may be more segregated trophically (or spatially) than monomorphic species in polar and temperate environments, but not in the tropics. The environmental homogeneity of tropics and their unpredictable foraging grounds could be key differences explaining these results. Most tropical seabirds are entirely pelagic and virtually no coastal species were tested, limiting the ability of stable isotopes to identify foraging segregation. Further studies incorporating more diverse tropical marine avifauna would contribute to our understanding of the mechanism that results in sexual size dimorphism.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2013.09.011.

References

Acha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M., Bava, J., 2004. Marine fronts at the continental shelves of austral South America. J. Mar. Syst. 44, 83–105.

Ainley, D.G., Boekelheide, R.J., 1983. An ecological comparision of oceanic seabird communities of South Pacific Ocean. Stud. Avian Biol. 8, 2–23.

Ainley, D.G., Ribic, C.A., Ballard, G., Heath, S., Gaffney, I., Karl, B.J., Barton, K.J., Wilson, P.R., Webb, S., 2004. Geographic structure of Adélie penguin populations: overlap in colony-specific foraging areas. Ecol. Monogr. 74, 159–178.

Amadon, D., 1959. The significance of sexual differences in size among birds. Proc. Am. Philos. Soc. 103, 531–536.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA for PRIMER: A Guide to Software and Statistical Methods. PRIMER-E, UK.

Andersson, M., 1994. Sexual Selection. Princeton University Press, Princeton.

Andersson, M., Norberg, R.A., 1981. Evolution of reversed sexual size dimorphism and role partitioning among raptors, with a size scaling of flight performance. Biol. J. Linnean Soc. 15, 105–130.

Ashmole, N.P., Ashmole, M.J., 1967. Comparative feeding ecology of sea birds of a tropical oceanic island. Peabody Mus. Nat. Hist. 24, 1–131.

Awkerman, J.A., Hobson, K.A., Anderson, D.J., 2007. Isotopic (δ^{15}N and δ^{13}C) evidence for intersexual foraging differences and temporal variation in habitat use in Waved albatrosses. Can. J. Zool. 85, 273–279.

Ballance, L.T., Pitman, R.L., 1999. Foraging ecology of tropical seabirds. In: Adams, N.J., Slotow, R.H. (Eds.), Proceedings 22nd International Ornithology Congress, Durban. NHBS, Birdlife, South Africa, Johannesburg, pp. 2057–2071.

Ballance, L.T., Pitman, R.L., Reilly, S.B., 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. Ecology 78, 1502–1518.

Ballance, L.T., Pitman, R.L., Fiedler, P.C., 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. Prog. Oceanogr. 69, 360–390.

Barrett, R.T., Camphuysen, K., Anker-Nilssen, T., Chardine, J.W., Furness, R.W., Garthe, S., Huppop, O., Leopold, M.F., Montevecchi, W.A., Veit, R.R., 2007. Diet studies of seabirds: a review and recommendations. ICES J. Mar. Sci. 64, 1675–1691.

Bearhop, S., Thompson, D.R., Phillips, R.A., Waldron, S., Hamer, K.C., Gray, C.M., Votier, S.C., Ross, B.P., Furness, R.W., 2001. Annual variation in Great skua diets: the importance of commercial fisheries and predation on seabirds revealed by combining dietary analyses. Condor 103, 802–809.

Bearhop, S., Waldron, S., Votier, S.C., Furness, R.W., 2002. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. Physiol. Biochem. Zool. 75, 451–458.

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., Macleod, H., 2004. Determining trophic niche width: a novel approach using stable isotope analysis. J. Anim. Ecol. 73, 1007–1012.

Bearhop, S., Phillips, R., McGill, R., Cherel, Y., Dawson, D., Croxall, J., 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. Mar. Ecol. Prog. Ser. 311, 157–164.

Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Stat. Soc. 57, 289–300.

Bugoni, L., McGill, R.A.R., Furness, R.W., 2010. The importance of pelagic longline fishery discards for a seabird community determined through stable isotope analysis. J. Exp. Mar. Biol. Ecol. 391, 190–200.

Carscadden, J., Montevecchi, W.A., Davoren, G.K., Nakashima, B.S., 2002. Trophic relationships among Capelin (*Mallotus villosus*) and seabirds in a changing ecosystem. ICES J. Mar. Sci. 59, 1027–1033.

Catry, T., Ramos, J.A., Corre, M., Kojadinovic, J., Bustamante, P., 2008. The role of stable isotopes and mercury concentrations to describe seabird foraging ecology in tropical environments. Mar. Biol. 155, 637–647.

Cherel, Y., Corre, M., Jaquemet, S., Ménard, F., Richard, P., Weimerskirch, H., 2008. Resource partitioning within a tropical seabird community: new information from stable isotopes. Mar. Ecol. Prog. Ser. 366, 281–291.

Cook, T.R., Lescroël, A., Cherel, Y., Kato, A., Bost, C.A., 2013. Can foraging ecology drive the evolution of body size in a diving endotherm? PloS ONE 8, e56297.

Croxall, J.P., 1995. Sexual size dimorphism in seabirds. Oikos 73, 399–403.

Cruz, L.L., McGill, R.A.R., Goodman, S.J., Hamer, K.C., 2012. Stable isotope ratios of a tropical marine predator: confounding effects of nutritional status during growth. Mar. Biol. 159, 873–880.

Diamond, A.W., 1983. Feeding overlap in some tropical and temperate seabird communities. Stud. Avian Biol. 8, 24–46.

Duffy, D.C., Jackson, S., 1986. Diet studies of seabirds: a review of methods. Colon. Waterbirds 9, 1–17.

Ehrich, D., Tarroux, A., Stien, J., Lecompte, N., Killengreen, S., Berteaux, D., Yoccoz, N.G., 2010. Stable isotope analysis: modelling lipid normalization for muscle and eggs from Arctic mammals and birds. Methods Ecol. Evol. 2, 66–76.

Ericson, P.G.P., Britton, A., Eizanowski, C.L., Johansson, T.A., K llersj , U.F., Ohlson, M., Parsons, J.I., Zuccon, T.J., Mayr, G., 2006. Diversification of Neoaves: integration of molecular sequence data and fossils. Biol. Lett. 2, 543–547.

Fairbairn, D.J., Shine, R., 1993. Patterns of sexual size dimorphism in seabirds of the Southern Hemisphere. Oikos 68, 139–145.

Fairbairn, D.J., Blanckenhorn, W.U., Székely, T., 2007. Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, Oxford.

Forero, M.G., Hobson, K.A., Bortolotti, G.R., Donázar, J.A., Bertellotti, M., Blanco, G., 2002. Food resource utilisation by the Magellanic penguin evaluated through stable-isotope analysis: segregation by sex and age and influence on offspring quality. Mar. Ecol. Prog. Ser. 234, 289–299.

Forero, M.G., Bortolotti, G.R., Hobson, K.A., Donazar, J.A., Bertelloti, M., Blanco, G., 2004. High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach. J. Anim. Ecol. 73, 789–801.

Forero, M.G., González-Solís, J., Hobson, K.A., Donázar, J.A., Bertellotti, M., Blanco, G., Bortolotti, G.R., 2005. Stable isotopes reveal trophic segregation by sex and age in the Southern giant petrel in two different food webs. Mar. Ecol. Prog. Ser. 296, 107–113.

Fridolfsson, A.K., Ellegren, H., 1999. A simple and universal method for molecular sexing of non-ratite birds. J. Avian Biol. 30, 116–121.

Fritz, S.A., Purvis, A., 2010. Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. Conserv. Biol. 24, 1042–1051.

Gibbons, J.W., Lovich, J.E., 1990. Sexual dimorphism in turtles with emphasis on the Slider turtle (*Trachemys scripta*). Herpetol. Monogr. 4, 1–29.

González-Solís, J., Croxall, J.P., 2005. Differences in foraging behaviour and feeding ecology in giant petrels. In: Ruckstuhl, K.E., Neuhaus, P. (Eds.), Sexual Segregation in Vertebrates: Ecology of the Two Sexes. Cambridge University Press, Cambridge, pp. 92–111.

González-Solís, J., Croxall, J.P., Wood, A.G., 2000. Sexual dimorphism and sexual segregation in foraging strategies of Northern giant petrels *Macronectes halli* during the incubation period. Oikos 90, 390–398.

Graham, B.S., Koch, P.L., Newsome, S.D., McMahon, K.W., Aurioles, D., 2010. Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West, J.B., Bowen, G.J., Dawson, T.E., Tu, K.P. (Eds.), Isoscapes. Springer, Dordrecht, pp. 299–318.

Grebmeir, J.M., Harrison, N.M., 1992. Seabird feeding on benthic amphipods facilitated by Gray whale activity in the northern Bering Sea. Mar. Ecol. Prog. Ser. 80, 125–133.

Harding, A.M.A., Hobson, K.A., Walkusz, W., Dmoch, K., Karnovsky, N.J., Pelt, T.I., Lifjeld, J.T., 2008. Can stable isotope (δ^{13}C and δ^{15}N) measurements of Little auk (*Alle alle*) adults and chicks be used to track changes in high-Arctic marine foodwebs? Polar Biol. 31, 725–733.

Harrison, C.S., Hida, T.S., Seki, M.P., 1983. The diet of the Brown booby *Sula leucogaster* and Masked booby *Sula dactylatra* on Rose Atoll, Samoa. Ibis 126, 588–590.

Hedd, A., Montevecchi, W.A., 2006. Diet and trophic position of Leach's storm-petrel *Oceanodroma leucorhoa* during breeding and moult, inferred from stable isotope analysis of feathers. Mar. Ecol. Prog. Ser. 322, 291–301.

Hobson, K.A., 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120, 314–326.

Hobson, K.A., 2011. Isotopic ornithology: a perspective. J. Ornithol. 152, 49–66.

Hobson, K.A., Bond, A.L., 2012. Extending an indicator: year-round information on seabird trophic ecology from multiple-tissue stable-isotope analyses. Mar. Ecol. Prog. Ser. 461, 233–243.

Hobson, K.A., Clark, R.G., 1992. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. Condor 94, 189–197.

Hobson, K.A., Welch, H.E., 1992. Determination of trophic relationships within a high Arctic marine food web using δ^{13}C and δ^{15}N analysis. Mar. Ecol. Prog. Ser. 84, 9–18.

Hobson, K.A., Piatt, J.F., Pitochellit, J., 1994. Using stable isotopes to determine seabird trophic relationships. J. Anim. Ecol. 63, 786–798.

Hobson, K.A., Fisk, A., Karnovsky, N., Holst, M., Gagnon, J., Fortier, M., 2002. A stable isotope (δ^{13}C, δ^{15}N) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. Deep Sea Res. II 49, 5131–5150.

Hyrenbach, D.K., Veit, R.R., Weimerskirch, H., Hunt-Jr, G.L., 2006. Seabird association with mesoscale eddies: the subtropical Indian Ocean. Mar. Ecol. Prog. Ser. 324, 271–279.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Mooers, A.O., 2012. The global diversity of birds in space and time. Nature 491, 444–448.

Karnovsky, N., Hobson, K.A., Iverson, S., 2012. From lavage to lipids: estimating diets of seabirds. Mar. Ecol. Prog. Ser. 451, 263–284.

Kelly, J.F., 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can. J. Zool. 78, 1–27.

Krüger, O., 2005. The evolution of sexual size dimorphism in hawks, falcons and owls: a comparative study. Evol. Ecol. 19, 467–486.

Lavoie, R.A., Rail, J.F., Lean, S., 2012. Diet composition of seabirds from Corossol Island, Canada, using direct dietary and stable isotope analyses. Waterbirds 35, 402–419.

Lewis, S., Benvenuti, S., DallAntonia, L., Money, L., Sherratt, T.N., Wanless, S., Hamer, K.C., 2002. Sex-specific behaviour in a monomorphic seabird. Proc. R. Soc. Lond. B 269, 1687–1693.

Longhurst, A.R., Pauly, D., 1987. Ecology of Tropical Oceans. Academic Press, California.

Maddison, W.P., Maddison, D.R., 2010. Mesquite: a modular system for evolutionary analysis, version 2.74. January 2013. Available from URL: http://mesquiteproject.org.

Magrath, M.J.L., Van-Lieshout, E., Pen, I., Visser, G.H., Komdeur, J., 2007. Estimating expenditure on male and female offspring in a sexually size-dimorphic bird: a comparison of different methods. J. Anim. Ecol. 76, 1169–1180.

Mancini, P.L., Hobson, K.A., Bugoni, L., 2013. The role of body size in shaping the trophic structure of tropical seabird communities. Mar. Ecol. Prog. Ser. http://dx.doi.org/10.3354/meps10589 (in press).

Masello, J.F., Mundry, R., Poisbleau, M., Demongin, L., Voigt, C.C., Wikelski, M., Quillfeldt, P., 2010. Diving seabirds share foraging space and time within and among species. Ecosphere 1, art19.

McMahon, K.W., Hamady, L., Thorrold, S.R., 2013. A review of ecogeochemistry approaches to estimating movements of marine animals. Limnol. Oceanogr. 58, 697–714.

Mill, A.C., Sweeting, C., Barnes, C., Al-Habsi, S., MacNeil, M.A., 2008. Mass-spectrometer bias in stable isotope ecology. Limnol. Oceanogr. Methods 6, 34–39.

Navarro, J., Kaliontzopoulou, A., González-Solís, J., 2009. Sexual dimorphism in bill morphology and feeding ecology in Cory's shearwater (*Calonectris diomedea*). Zoology 112, 128–138.

Nelson, B.J., 2005. Pelicans, Cormorants, and Their Relatives. Oxford University Press, New York.

Newsome, S.D., Martinez-del-Rio, C., Bearhop, S., Phillips, D.L., 2007. A niche for isotopic ecology. Front. Ecol. Environ. 5, 429–436.

Nisbet, I.C.T., Montoya, J.P., Burger, J., Hatch, J.J., 2002. Use of stable isotopes to investigate individual differences in diets and mercury exposures among Common terns *Sterna hirundo* in breeding and wintering grounds. Mar. Ecol. Prog. Ser. 242, 267–274.

Obst, B.S., Hunt Jr., G.L., 1990. Marine birds feed at Gray whale mud plumes in the Bering Sea. Auk 107, 678–688.

Owen, J.C., Sogge, M.K., Kern, M.D., 2005. Habitat and sex differences in physiological condition of breeding Southwestern willow flycatchers (*Empidonax trailli extimus*). Auk 122, 1261–1270.

Paredes, R., Jones, I.L., Boness, D.J., Tremblay, Y., Renner, M., 2008. Sex-specific differences in diving behaviour of two sympatric Alcini species: Thick-billed murres and Razorbills. Can. J. Zool. 86, 610–622.

Phillips, R.A., Silk, J.R.D., Phalan, B., Catry, P., Croxall, J.P., 2004. Seasonal sexual segregation in two *Thalassarche* albatrosses: competitive exclusion, reproductive role specialization or foraging niche divergence? Proc. R. Soc. Lond. B 271, 1283–1291.

Phillips, R.A., McGill, R.A.R., Dawson, D.A., Bearhop, S., 2011. Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. Mar. Biol. 158, 2199–2208.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718.
Quillfeldt, P., McGill, R.A.R., Masello, J.F., Weiss, F., Strange, I.J., Brickle, P., Furness, R.W., 2008. Stable isotope analysis reveals sexual and environmental variability and individual consistency in foraging of Thin-billed prions. Mar. Ecol. Prog. Ser. 373, 137–148.
Ramos, R., González-Solís, J., Forero, M.G., Moreno, R., Gómez-Díaz, E., Ruiz, X., Hobson, K.A., 2009. The influence of breeding colony and sex on mercury, selenium and lead levels and carbon and nitrogen stable isotope signatures in summer and winter feathers of *Calonectris* shearwaters. Oecologia 159, 345–354.
Ridoux, V., 1994. The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. Mar. Ornithol. 22, 1–192.
Roby, D.D., Brinck, K.L., Nettleship, D.N., 1981. Measurements, chick meals and breeding distribution of Dovekies (*Alle alle*) in northwest Greenland. Arctic 34, 241–248.
Russell, R.W., Harrison, N.M., Hunt-Jr, G.L., 1999. Foraging at a front: hydrography, zooplankton, and avian planktivory in the northern Bering Sea. Mar. Ecol. Prog. Ser. 182, 77–93.
Schreiber, E.A., Burger, J. (Eds.), 2002. Biology of Marine Birds. CRC Press, Boca Raton, Florida.
Selander, R.K., 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68, 113–151.
Shine, R., 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Q. Rev. Biol. 64, 419–461.
Stauss, C., Bearhop, S., Bodey, T.W., Garthe, S., Gunn, C., Grecian, W.J., Inger, R., Knight, M.E., Newton, J., Patrick, S.C., Phillips, R.A., Waggitt, J.J., Votier, S.C., 2012. Sex-specific foraging behaviour in Northern gannets *Morus bassanus*: incidence and implications. Mar. Ecol. Prog. Ser. 457, 151–162.
Sydeman, W.J., Hobson, K.A., Ox, S.N., Pyle, P., McLaren, E.B., 1997. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. Condor 99, 327–336.
Weimerskirch, H., 2007. Are seabirds foraging for unpredictable resources? Deep Sea Res. Part II 54, 211–223.
Weimerskirch, H., Salamolard, M., Sarranzin, F., Jouventin, P., 1993. Foraging strategy of Wandering albatrosses through the breeding season: a study using satellite telemetry. Auk 110, 325–342.
Weimerskirch, H., Le Corre, M., Ropert-Coudert, Y., Kato, A., Marsac, F., 2006. Sex-specific foraging behavior in a seabird with reversed sexual dimorphism, the Red-footed booby. Oecologia 146, 681–691.
Weimerskirch, H., Shaffer, S.A., Tremblay, Y., Costa, D.P., Gadenne, H., Kato, A., Ropert-Coudert, Y., Sato, K., Aurioles, D., 2009. Species- and sex-specific differences in foraging behaviour and foraging zones in Blue-footed and Brown boobies in the Gulf of California. Mar. Ecol. Prog. Ser. 391, 267–278.
Wikelski, M., Kays, R.W., Kasdin, N.J., Thorup, K., Smith, J.A., Swenson, G.W., 2007. Going wild: what a global small-animal tracking system could do for experimental biologists. J. Exp. Biol. 210, 181–186.
Wilson, R.P., Vandenabeele, S.P., 2012. Technological innovation in archival tags used in seabird research. Mar. Ecol. Prog. Ser. 451, 245–262.
Wilson, R.P., Grémillet, D., Syder, J., Kierspel, M.A.M., Garthe, S., Weimerskirch, H., Schäfer-Neth, C., Scolaro, J.A., Bost, C.A., Plötz, J., Nel, D., 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. Mar. Ecol. Prog. Ser. 228, 241–261.
Wojczulanis, K., Jakubas, D., Walkusz, W., Wennerberg, L., 2006. Differences in food delivered to chicks by males and females of Little auks (*Alle alle*) on South Spitsbergen. J. Ornithol. 147, 543–548.
Wolf, N., Carleton, S.A., Martínez-del-Rio, C., 2009. Ten years of experimental animal isotopic ecology. Funct. Ecol. 23, 17–26.
Young, H.S., Shaffer, S.A., McCauley, D.J., Foley, D.G., Dirzo, R., Block, B.A., 2010a. Resource partitioning by species but not sex in sympatric boobies in the central Pacific Ocean. Mar. Ecol. Prog. Ser. 403, 291–301.
Young, H.S., McCauley, D.J., Dirzo, R., Dunbar, R.B., Shaffer, S.A., 2010b. Niche partitioning among and within sympatric tropical seabirds revealed by stable isotope analysis. Mar. Ecol. Prog. Ser. 416, 285–294.
Zar, J.H., 2010. Biostatistical Analysis, 5th ed. Prentice-Hall, Upper Saddle River NJ.

Appendix 1. Literature review of stable isotope ratios, in relation to sexual size dimorphism in seabirds and trophic/spatial segregation, during the breeding season. D = dimorphism, M = monomorphism, T = tropical, NT = No tropical, B= blood, F = feather, M = muscle, P = plasma. Order: Cha = Charadriiformes, Pha = Phaethontiformes, Pro = Procellariiformes, Sph = Sphenisciformes, Sul = Suliformes, * = segregation only by δ^{13}C values.

Common name	Scientific name	Order	SSD	SI Dif sex	Region	Tissue	Area	References
Razorbill	*Alca torda*	Cha	M	yes	NT	B	Gulf of St. Lawrence, Canada	Lavoie et al. (2012)
Dovekie	*Alle alle*	Cha	D	no	NT	B	Spitsbergen, Norway	Harding et al. (2008)
Dovekie	*Alle alle*	Cha	D	no	NT	M	Northwater Polynya, Canada	Hobson and Bond (2012)
Black noddy	*Anous minutus*	Cha	M	no	T	B	Fernando de Noronha Archipelago, Brazil	This study
Black noddy	*Anous minutus*	Cha	M	no	T	B	São Pedro and São Paulo Archipelago	This study
Brown noddy	*Anous stolidus*	Cha	M	no	T	B	Abrolhos Archipelago, Brazil	This study
Brown noddy	*Anous stolidus*	Cha	M	no	T	B	Atol das Rocas, Brazil	This study
Brown noddy	*Anous stolidus*	Cha	D	no	T	B	São Pedro and São Paulo Archipelago	This study
Marble murrelet	*Brachyramphus*	Cha	M	no	NT	F	Monterey Bay, USA	Becker et al. (2007)

	marmoratus							
Brown skua	*Catharacta a. lonnbergi*	Cha	D	no	NT	B	South Georgia Is.	Anderson et al. (2008)
Black guillemot	*Cepphus grylle*	Cha	M	yes	NT	M	Northwater Polynya, Canada	Hobson and Bond (2012)
Tufted puffin	*Fratercula cirrhata*	Cha	D	no	NT	B	Kodiak Is., Alaska	Williams et al. (2008)
Herring gull	*Larus argentatus*	Cha	D	yes	NT	B	Gulf of St. Lawrence, Canada	Lavoie et al. (2012)
Audouin's gull*	*Larus audouinii*	Cha	M	yes	T	B	Erbo Delta, Spain	Navarro et al. (2010)
Glaucos gull	*Larus hyperboreus*	Cha	D	yes	NT	M	Northwater Polynya, Canada	Hobson and Bond (2012)
Great black-backed gull	*Larus marinus*	Cha	D	yes	NT	B	Gulf of St. Lawrence, Canada	Lavoie et al. (2012)
Sooty tern	*Onychoprion fuscatus*	Cha	D	no	T	B	Atol das Rocas, Brazil	This study
Ivory gull	*Pagophila eburnea*	Cha	M	no	NT	M	Northwater Polynya, Canada	Hobson and Bond (2012)
Black-legged kittiwake	*Rissa tridactyla*	Cha	D	no	NT	M	Northwater Polynya, Canada	Hobson and Bond (2012)
Black-legged kittiwake	*Rissa tridactyla*	Cha	D	no	NT	B	Gulf of St. Lawrence, Canada	Lavoie et al. (2012)
Common tern	*Sterna hirundo*	Cha	M	yes	NT	F	Massachusstts, USA	Nisbet et al. (2002)
Arctic tern	*Sterna paradisaea*	Cha	D	no	NT	B	Nasarvuallik, Nunavut, Canada	Boadway (2012)
Thick-billed murre	*Uria lomvia*	Cha	M	yes	NT	M	Northwater Polynya, Canada	Hobson and Bond (2012)
Thick-billed murre	*Uria lomvia*	Cha	M	no	NT	P	Nunavut, Canada	Woo et al. (2008)

Red-billed tropicbird	*Phaethon aethereus*	Pha	D	no	T	B	Abrolhos Archipelago, Brazil	This study
Cory's shearwater	*Calonectris borealis*	Pro	D	yes	NT	B, F	Chafarinas Archipelago, Mediterranean Sea	Navarro et al. (2009a)
Scopoli's shearwater*	*Calonectris d. diomedea*	Pro	D	yes	NT	F	Mediterranean Archipelago	Ramos et al. (2009)
Scopoli's shearwater	*Calonectris d. diomedea*	Pro	D	yes	NT	B, F	Chafarinas Archipelago, Mediterranean Sea	Navarro et al. (2009a)
Cory's shearwater	*Calonectris d. borealis*	Pro	D	no	T	B	Gran Canaria, Canary Is., NE Atlantic Ocean	Navarro et al. (2009b)
Cory's shearwater*	*Calonectris d. borealis*	Pro	D	yes	NT	F	Canary Is. Northeast Atlantic Ocean,	Ramos et al. (2009)
Cape Verde shearwater*	*Calonectris edwardsii*	Pro	D	yes	NT	F	Cape Verde Archipelago, NE Atlantic Ocean	Ramos et al. (2009)
Wandering albatross*	*Diomedea exulans*	Pro	D	yes	NT	B	Bird Is., South Georgia Is.	Ceia et al. (2012)
Wandering albatross	*Diomedea exulans*	Pro	D	no	NT	B	South Georgia Is.	Phillips et al. (2011)
Northern fulmar	*Fulmarus glacialis*	Pro	D	yes	NT	M	Northwater Polynya, Canada	Hobson and Bond (2012)
Southern giant petrel	*Macronectes giganteus*	Pro	D	yes	NT	B	South Georgia Is.	Forero et al. (2005)

Southern giant petrel	*Macronectes giganteus*	Pro	D	yes	NT	B	Patagonia, Argentina	Forero et al. (2005)
Southern giant petrel	*Macronectes giganteus*	Pro	D	yes	NT	B	Observatorio Is., Argentina	Rey et al. (2012)
Southern giant petrel	*Macronectes giganteus*	Pro	D	yes	NT	B	South Georgia Is.	Rey et al. (2012)
Northern giant petrel	*Macronectes halli*	Pro	D	yes	NT	B	South Georgia Is.	González-Solís and Croxall (2005)
Northern giant petrel*	*Macronectes halli*	Pro	D	yes	NT	B	South Georgia Is.	Phillips et al. (2011)
Leach's storm-petrel	*Oceanodroma leucorhoa*	Pro	M	no	NT	F	Newfoundland, Canada	Hedd and Montevecchi (2006)
Thin-billed prion	*Pachyptila belcheri*	Pro	M	yes	NT	B	Falkland/Malvinas Is.	Quillfeldt et al. (2008)
Antarctic prion	*Pachyptila desolata*	Pro	M	no	NT	B	South Georgia Is.	Phillips et al. (2011)
South Georgian diving-petrel	*Pelecanoides georgicus*	Pro	M	no	NT	B	South Georgia Is.	Phillips et al. (2011)
Common diving petrel	*Pelecanoides urinatrix*	Pro	M	no	NT	B	South Georgia Is.	Phillips et al. (2011)
Waved albatross*	*Phoebastria irrorata*	Pro	D	yes	T	B	Galapagos Is.	Awkerman et al. (2007)

Cook's petrel	*Pterodroma cookii*	Pro	M	yes	NT	B	New Zealand	Rayner et al. (2008)
Black-browed albatross	*Thalassarche melanophris*	Pro	D	no	NT	B	South Georgia Is.	Phillips et al. (2011)
King penguin	*Aptenodytes patagonicus*	Sph	D	yes	NT	B	Crozet Archipelago, Indian Ocean	Vaillant et al. 2013
Macaroni penguin	*Eudyptes chrysolophus*	Sph	D	no	NT	B	South Georgia Is.	Bearhop et al. (2006)
Southern rockhopper penguin	*Eudyptes chrysocome*	Sph	D	yes	NT	B	Falkland/Malvinas Is. Atlantic Ocean	Ludynia et al. (2013)
Little penguin	*Eudyptula minor*	Sph	M	no	NT	B	Philip Is., Australia	Chiaradia et al. (2011)
Little penguin	*Eudyptula minor*	Sph	M	no	NT	B	St. Kilda Is., Scotland	Chiaradia et al. (2011)
Northern rockhopper penguin	*Eudyptes moseleyi*	Sph	D	yes	NT	B	Tristan da Cunha Arch., Atlantic Ocean	Booth and McQuaid (2013)
Gentoo penguin	*Pygoscelis papua*	Sph	D	yes	NT	B	South Georgia Is., Atlantic Ocean	Bearhop et al. (2006)
Magellanic penguin	*Spheniscus magellanicus*	Sph	D	yes	NT	B	Patagonia, Argentina, in 9 different colonies	Forero et al. (2002)
Great frigatebird	*Fregata minor*	Sul	D	no	T	B	Europa Is., Indian Ocean	Cherel et al. (2008)
Great frigatebird	*Fregata minor*	Sul	D	no	T	B, F	Palmyra Atoll, Pacific Ocean	Young et al. (2010a)

Northern gannet	*Morus bassanus*	Sul	M	yes	NT	B	Grassholm, UK, Atlantic Ocean	Stauss et al. (2012)
South Georgian shag	*Phalacrocorax a. georgianus*	Sul	D	yes	NT	B	South Georgia Is., Atlantic Ocean	Bearhop et al. (2006)
Imperial shag	*Phalacrocorax atriceps*	Sul	D	yes	NT	B	Falkland/Malvinas Is., Atlantic Ocean	Michalik et al. (2012)
Blue-eyed shag*	*Phalacrocorax verrucosus*	Sul	D	yes	NT	B	Kerguelen Is., Indian Ocean	Cook et al. (2013)
Masked booby	*Sula dactylatra*	Sul	D	no	T	B, F	Palmyra Atoll, Pacific Ocean	Young et al. (2010b)
Masked booby	*Sula dactylatra*	Sul	D	no	T	B, F	Palmyra Atoll, Pacific Ocean	Young et al. (2010a)
Masked booby	*Sula dactylatra*	Sul	D	no	T	B	Abrolhos Archipelago, Brazil	This study
Masked booby	*Sula dactylatra*	Sul	D	no	T	B	Fernando de Noronha, Brazil	This study
Masked booby	*Sula dactylatra*	Sul	D	no	T	B	Atol das Rocas, Brazil	This study
Brown booby	*Sula leucogaster*	Sul	D	no	T	B	Baja California, Mexico	Weimerskirch et al. (2009)
Brown booby	*Sula leucogaster*	Sul	D	yes	T	B, F	Palmyra Atoll, Pacific Ocean	Young et al. (2010a)
Brown booby	*Sula leucogaster*	Sul	D	no	T	B	Abrolhos Archipelago	This study
Brown booby	*Sula leucogaster*	Sul	D	no	T	B	Fernando de Noronha, Brazil	This study
Brown booby	*Sula leucogaster*	Sul	D	no	T	B	Atol das Rocas, Brazil	This study

Brown booby	*Sula leucogaster*	Sul	D	no	T	B	São Pedro and São Paulo Arch., Brazil	This study
Blue-footed booby	*Sula nebouxii*	Sul	D	no	T	B	Baja California, Mexico	Weimerskirch et al. (2009)
Blue-footed booby	*Sula nebouxii*	Sul	D	no	T	B	Galapagos Is., Ecuador	Cruz et al. (2012)
Red-footed booby	*Sula sula*	Sul	D	yes	T	B	Europa Is. Indian Ocean	Cherel et al. (2008)
Red-footed booby	*Sula sula*	Sul	D	no	T	B, F	Palmyra Atoll, Pacific Ocean	Young et al. (2010a)
Red-footed booby	*Sula sula*	Sul	D	no	T	B, F	Palmyra Atoll, Pacific Ocean	Young et al. (2010b)

References

Anderson, O.R.J., Phillips, R.A., Shore, R.F., McGill, R.A.R., McDonald, R.A., Bearhop, S., 2008. Diet, individual specialisation and breeding of Brown skuas (*Catharacta antarctica lonnbergi*): an investigation using stable isotopes. Polar Biol. 32, 27–33.

Awkerman, J.A., Hobson, K.A., Anderson, D.J., 2007. Isotopic (δ^{15}N and δ^{13}C) evidence for intersexual foraging differences and temporal variation in habitat use in waved albatrosses. Can. J. Zool. 85, 273–279.

Bearhop, S., Phillips, R., McGill, R., Cherel, Y., Dawson, D., Croxall, J., 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. Mar. Ecol. Prog. Ser. 311, 157–164.

Becker, B., Peery, M., Beissinger, S., 2007. Ocean climate and prey availability affect the trophic level and reproductive success of the Marbled murrelet, an endangered seabird. Mar. Ecol. Prog. Ser. 329, 267–279.

Boadway, K.A., 2012. Finding the "Arctic" in the Arctic tern: breeding biology and diet across the latitudinal range of an iconic seabird. University of New Brunswick, Department of Biology, p. 380.

Booth, J., McQuaid, C., 2013. Northern rockhopper penguins prioritise future reproduction over chick provisioning. Mar. Ecol. Prog. Ser. 486, 289–304.

Ceia, F.R., Phillips, R.A., Ramos, J.A., Cherel, Y., Vieira, R.P., Richard, P., Xavier, J.C., 2012. Short- and long-term consistency in the foraging niche of Wandering albatrosses. Mar. Biol. 159, 1581–1591.

Cherel, Y., Corre, M., Jaquemet, S., Ménard, F., Richard, P., Weimerskirch, H., 2008. Resource partitioning within a tropical seabird community: new information from stable isotopes. Mar. Ecol. Prog. Ser. 366, 281–291.

Chiaradia, A., Forero, M.G., Hobson, K.A., Swearer, S.E., Hume, F., Renwick, L., Dann, P., 2011. Diet segregation between two colonies of Little penguins *Eudyptula minor* in southeast Australia. Austral Ecol. 37, 610–619.

Cook, T.R., Lescroël, A., Cherel, Y., Kato, A., Bost, C.A., 2013. Can foraging ecology drive the evolution of body size in a diving endotherm? PloS ONE 8, e56297.

Cruz, L.L., McGill, R.A.R., Goodman, S.J., Hamer, K.C., 2012. Stable isotope ratios of a tropical marine predator: confounding effects of nutritional status during growth. Mar. Biol. 159, 873–880.

Forero, M.G., González-Solís, J., Hobson, K.A., Donázar, J.A., Bertellotti, M, Blanco, G., Bortolotti, G.R., 2005. Stable isotopes reveal trophic segregation by sex and age in the Southern giant petrel in two different food webs. Mar. Ecol. Prog. Ser. 296, 107–113.

Forero, M., Hobson, K.A., Bortolotti, G., Donázar, J., Bertellotti, M., Blanco, G., 2002. Food resource utilisation by the Magellanic penguin evaluated through stable-isotope analysis: segregation by sex and age and influence on offspring quality. Mar. Ecol. Prog. Ser. 234, 289–299.

González-Solís, J., Croxall, J.P., 2005. Differences in foraging behaviour and feeding ecology in giant petrels. In: Ruckstuhl KE, Neuhaus P (Eds) Sexual segregation in vertebrates: ecology of the two sexes. Cambridge University Press, Cambridge, pp. 92–111.

Harding, A.M.A., Hobson, K.A., Walkusz, W., Dmoch, K., Karnovsky, N.J., Pelt, T.I., Lifjeld, J.T., 2008. Can stable isotope (δ^{13}C and δ^{15}N) measurements of Little auk (*Alle alle*) adults and chicks be used to track changes in high-Arctic marine foodwebs? Polar Biol. 31, 725–733.

Hedd, A., Montevecchi, W.A., 2006. Diet and trophic position of Leach's storm-petrel *Oceanodroma leucorhoa* during breeding and moult, inferred from stable isotope analysis of feathers. Mar. Ecol. Prog. Ser. 322, 291–301.

Hobson, K.A., Bond, A.L., 2012. Extending an indicator: year-round information on seabird trophic ecology from multiple-tissue stable-isotope analyses. Mar. Ecol. Prog. Ser. 461, 233–243.

Lavoie, R.A., Rail, J.F., Lean, S., 2012. Diet composition of seabirds from Corossol Island, Canada, using direct dietary and stable isotope analyses. Waterbirds, 35, 402–419.

Ludynia, K., Dehnhard, N., Poisbleau, M., Demongin, L., Masello, J.F., Voigt, C.C., Quillfeldt, P., 2013. Sexual segregation in Rockhopper penguins during incubation. Anim. Behav. 85, 255–267.

Michalik, A., McGill, R.A.R., Noordwijk, H.J., Masello, J.F., Furness, R.W., Eggers, T., Quillfeldt, P., 2012. Stable isotopes reveal variable foraging behaviour in a colony of the Imperial shag *Phalacrocorax atriceps*: differences between ages, sexes and years. J. Ornithol. 154, 239–249.

Navarro, J., Oro, D., Bertolero, A., Genovart, M., Delgado, A., Forero, M.G., 2010. Age and sexual differences in the exploitation of two anthropogenic food resources for an opportunistic seabird. Mar. Biol. 157, 2453–2459.

Navarro, J., Forero, M.G., González-Solís, J., Igual, J.M., Bécares, J., Hobson, K.A., 2009a. Foraging segregation between two closely related shearwaters breeding in sympatry. Biol. Lett. 5, 545–548.

Navarro, J., Kaliontzopoulou, A., González-Solís, J., 2009b. Sexual dimorphism in bill morphology and feeding ecology in Cory's shearwater (*Calonectris diomedea*). Zoology 112, 128–138.

Nisbet, I., Montoya, J., Burger, J., Hatch, J., 2002. Use of stable isotopes to investigate individual differences in diets and mercury exposures among Common terns *Sterna hirundo* in breeding and wintering grounds. Mar. Ecol. Prog. Ser. 242, 267–274.

Phillips, R.A., McGill, R.A.R., Dawson, D.A., Bearhop, S., 2011. Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. Mar. Biol. 158, 2199–2208.

Quillfeldt, P., McGill, R.A.R., Masello, J.F., Weiss, F., Strange, I.J., Brickle, P., Furness, R.W., 2008. Stable isotope analysis reveals sexual and environmental variability and individual consistency in foraging of Thin-billed prions. Mar. Ecol. Prog. Ser. 373, 137–148.

Ramos, R., González-Solís, J., Forero, M.G., Moreno, R., Gómez-Díaz, E., Ruiz, X., Hobson, K.A., 2009. The influence of breeding colony and sex on mercury, selenium and lead levels and carbon and nitrogen stable isotope signatures in summer and winter feathers of *Calonectris* shearwaters. Oecologia 159, 345–354.

Rayner, M. J., Hauber, M. E., Clout, M. N., Seldon, D. S., Van-Dijken, S., Bury, S., Phillips, R. A., 2008. Foraging ecology of the Cook's petrel *Pterodroma cookii* during the austral breeding season: a comparison of its two populations. Mar. Ecol. Prog. Ser. 370, 271–284.

Rey, A.R., Polito, M., Archuby, D., Coria, N., 2012. Stable isotopes identify age- and sex-specific dietary partitioning and foraging habitat segregation in Southern giant petrels breeding in Antarctica and southern Patagonia. Mar. Biol. 159, 1317–1326.

Stauss, C., Bearhop, S., Bodey, T.W., Garthe, S., Gunn, C., Grecian, W.J., Inger, R., Knight, M. E., Newton, J., Patrick, S.C., Phillips, R. A., Waggitt, J.J., Votier, S.C., 2012. Sex-specific foraging behaviour in Northern gannets *Morus bassanus*: incidence and implications. Mar. Ecol. Prog. Ser. 457, 151–162.

Vaillant, M., Bohec, C.L., Prud'Homme, O., Wienecke, B., Maho, Y., Kato, A., Ropert-Coudert, Y., 2013. How age and sex drive the foraging behaviour in the King penguin. Mar. Biol. 160, 1147–1156.

Weimerskirch, H., Shaffer, S., Tremblay, Y., Costa, D., Gadenne, H., Kato, A., Ropert-Coudert, Y., Sato, K., Aurioles, D., 2009. Species- and sex-specific differences in foraging behaviour and foraging zones in Blue-footed and Brown boobies in the Gulf of California. Mar. Ecol. Prog. Ser. 391, 267–278.

Williams, C.T., Iverson, S.J., Buck, C.L., 2008. Stable isotopes and fatty acid signatures reveal age- and stage-dependent foraging niches in Tufted puffins. Mar. Ecol. Prog. Ser. 363, 287–298.

Woo, K.J., Elliott, K.H., Davidson, M., Gaston, A.J., Davoren, G.K., 2008. Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. J. Anim. Ecol. 77, 1082–1091.

Young, H.S., McCauley, D.J., Dirzo, R., Dunbar, R.B., Shaffer, S.A., 2010a. Niche partitioning among and within sympatric tropical seabirds revealed by stable isotope analysis. Mar. Ecol. Prog. Ser. 416, 285–294.

Young, H.S., Shaffer, S.A., McCauley, D.J., Foley, D.G., Dirzo, R., Block, B.A., 2010b. Resource partitioning by species but not sex in sympatric boobies in the central Pacific Ocean. Mar. Ecol. Prog. Ser. 403, –301.