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High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach

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Summary

1. Food web interactions in animal communities can be investigated through the measurement of stable isotopes (e.g. $\delta^{15}N$, $\delta^{13}C$). We used this approach in a community of 14 species of seabirds breeding on the Argentinean Patagonian coast. Tissue samples were collected from nestling and adult seabirds, as well as prey, during three consecutive breeding seasons in 28 breeding colonies.

2. Relative to those in other temperate and polar regions, this seabird community showed a high degree of overlap in trophic level (TL) among species (93% of species within a TL range of 0·7) and also a comparatively high mean trophic level (4·1).

3. Relative positions of seabirds in relation to prey suggest that most species feed on pelagic fish and to a lesser extent on invertebrates. Stable isotope values of specialist feeders, Olrolg's (*Larus atlanticus*) and dolphin gulls (*Leucophaeus scoresbii*), which were previously assumed to feed mainly on crabs and sea lion excrement, respectively, suggested a broader diet than expected.

4. Based on stable isotope values of individuals, groups of phylogenetically related species generally showed a high degree of overlap within each group.

5. Given the degree of isotope overlap in this species-rich community, coexistence could be interpreted as a consequence of superabundance of food or species diversification in morphology and foraging strategies. The short range of trophic level makes these seabirds vulnerable to the reduction of fish stocks due either to commercial fishing or stochastic fluctuations.

Key-words: Argentinean coast of Patagonia, food relationships, seabird community, stable-isotopes.

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Introduction

Due to the importance of predator–prey relationships and their dynamics on the evolution and structure of animal communities, ecologists have developed numerous theoretical models involving different aspects of food webs and their influence on community parameters including stability, complexity, connectivity and equilibrium (e.g. Fussmann & Heber 2002; Melián & Bascompte 2002). Similarly, there has been considerable interest in investigating niche segregation / overlap, trophic ecology and parameters including species richness, relative abundance and spatial or temporal variation in the distribution of species in the community (e.g. Worm & Myers 2003). Such studies have emphasized that overlap in diets of different organisms and intra- and interspecific competition for food influence the evolution of species and communities. Progress in this field is limited as empirical evidence has lagged behind theoretical developments.

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Seabirds constitute an ideal model for studying trophic-ecology and food web dynamics. They occupy a wide range of ecological positions and also their communities vary greatly in species composition, abundance and size of colonies at even local scales (Coulson 2002). Other characteristics that make seabirds of special interest for studying trophic ecology are their extended chick-rearing periods, during which food requirements are high (Hamer, Shreiber & Burger 2002). Seasonality and, in many cases, unpredictability of food resources in marine ecosystems provide other characteristics that make seabirds valuable models for studying trophic ecology (Oro & Furness 2002; Simeone *et al*. 2002).

Conventional approaches to studying seabird diets, such as analyses of gut contents or regurgitation, have biases (Votier *et al*. 2003) and are often logistically difficult when several species are considered simultaneously and large sample sizes are desirable. An alternative involves the measurement of naturally occurring stable isotopes in consumers and their prey. This methodology has been applied to broad studies of trophic relationships in seabird communities (Hobson & Welch 1992; Hobson, Piatt & Pitocchelli 1994; Thompson *et al*. 1999), to more specific questions of temporal and spatial variability in diets (Bearhop *et al*. 2000; Brocher, Cherel & Hobson 2000; Hobson, Gilchrist & Falk 2002), and even to differences among individuals (Forero *et al*. 2002a, 2002b; Nisbet *et al*. 2002). The principle underlying this approach is that in marine systems, stable isotope ratios of nitrogen ($^{15}N/^{14}N$, denoted as $\delta^{15}N$) and carbon ($^{13}C/^{12}C$, $\delta^{13}C$) in consumers reflect those of their prey in a predictable manner (Michener & Schell 1994). Stable-nitrogen isotope values usually show a stepwise enrichment with each trophic level (Hobson & Welch 1992; Michener & Schell 1994). Stable-carbon isotope values show only a slight enrichment with trophic level, but $\delta^{13}C$ values can reveal spatial information on feeding location, including the relative use of inshore (more enriched) vs. offshore (depleted) habitats (France 1995; Hobson, Ambrose & Renauld 1995). Given that tissues have different isotopic turnover rates or represent different metabolic pathways (Tieszen *et al*. 1983; Hobson & Clark 1992; Hobson 1995), diets integrated over various temporal scales can be evaluated. Stable-isotope signatures of whole blood represent dietary information for a period of at least 4 weeks (Hobson & Clark 1992), thus being a valuable tissue for studying feeding ecology during discrete periods without the need to sacrifice birds (Hodum & Hobson 2000; Forero *et al*. 2002a, 2002b).

Our previous isotopic investigations revealed a high degree of intraspecific variation in diet of the Magellanic penguin [*Spheniscus magellanicus* (Forster)] in the Argentinean Patagonia (Forero *et al*. 2002a). However, the seabird community of that area is rich in species, and trophic relationships among them are unknown. Our work comprised a comprehensive sample of seabirds and their main prey to encompass potential sources of variation in the community (spatial, temporal and individual). Our overall objective was to describe the trophic structure of a complex assemblage of seabirds and determine the degree of ecological overlap/segregation among species. More specifically, we investigated trophic structure at multiple scales: (1) Patagonia in relation to seabird communities elsewhere; (2) within the Patagonian seabird community (including local food webs); and (3) among individuals within groups of phylogenetically related species.

Methods

STUDY AREA AND FIELD PROCEDURE

Fieldwork was undertaken in the Chubut province of the Argentinean Patagonia (Fig. 1), which covers about 1000 km of coast and numerous islands. This area is an example of a wide, fully open shelf that is highly affected by two major western boundary currents, Falklands' and Patagonian (Fig. 1). The Patagonian continental shelf is characterized by water-mass mixing caused by tide effects (Glorioso 1987). This condition produces several shelf frontal systems of high primary productivity (Bowman 1977). In total, 14 species (Table 1) nest along Chubut's coast, including one penguin, one petrel, five cormorants, three gulls, three terns and one skua. Most species are relatively abundant and have a wide distribution, but the Olrolg's gull [*Larus atlanticus* (Olrolg)], guanay cormorant [*Phalacrocorax bouganvillii* (Lesson)] and southern giant petrel [*Macronectes giganteus* (Gmelin)] have a restricted breeding area. Size and species composition of breeding colonies show a wide range of variation (Yorio *et al*. 1998).

Samples of whole blood of 1398 seabirds (adults and nestlings) from 14 species in 28 colonies were collected from November to January during three consecutive breeding seasons (1999–2001) (Table 1). Individuals were sampled from different nests arbitrarily chosen in each colony and about 1 mL of blood was extracted from the brachial or tarsal vein. Blood was transferred to vials containing 1·5 mL of 70% ethanol and stored at 20–25 °C until analysis of stable isotopes (Hobson, Gibbs & Gloutney 1997). In addition, we also sampled hybrid cormorants. The king cormorant [*P. atriceps albiventer* (Lesson)], blue-eyed cormorant [*P. atriceps atriceps* (King)] and guanay cormorant frequently hybridize. Although some authors have treated king and blue-eyed cormorants as different morphs of a single species (Rasmussen 1991), we considered them separately in the analysis. We classified an individual as a hybrid based on plumage characteristics following Malacalza (1991). The guanay cormorant is virtually extinct in this area, due probably to the generalized hybridization with congeneric species (Bertelloti *et al*. 2003). Only two individuals showing species-typical morphological features were located and sampled (Table 1).

On the basis of previous conventional dietary studies of this group of seabirds and very close species (Malacalza, Poretti & Bertelloti 1994; Yorio, Boersma & Swann 1996;

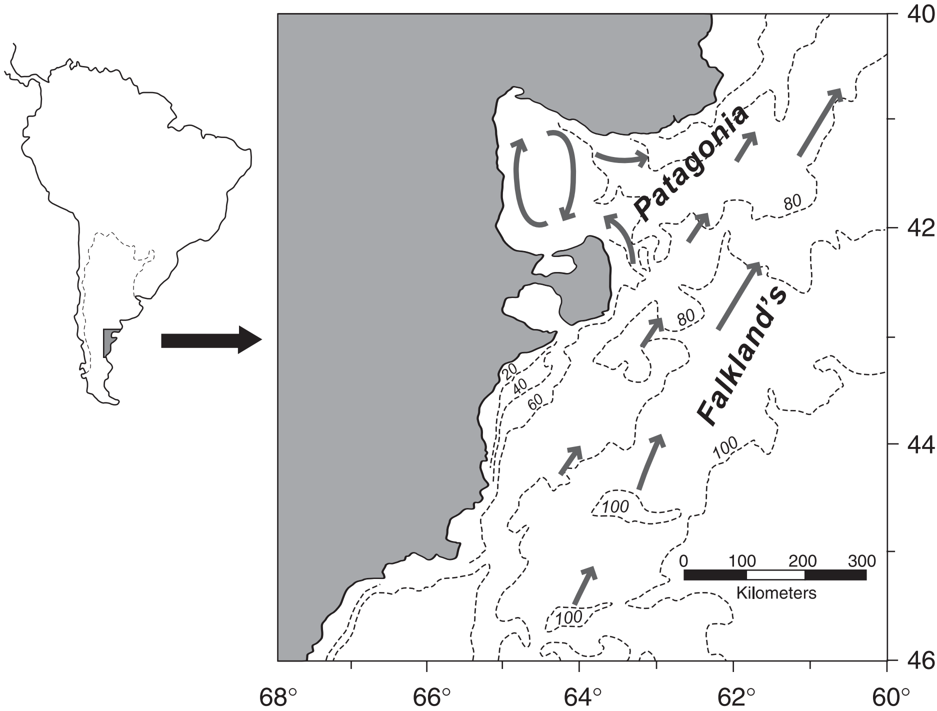

Fig. 1. Location, bathymetry (m) and the main oceanic currents of the Chubut province, Argentina.

Table 1. Sample sizes for seabird species in the Argentinean Patagonia

Species*	Seasons	Colonies	*n* adults	*n* chicks	*n* juveniles†	*n* total
OG	2	2		11		11
KG	2	10	29	200		229
DG	2	6	7	58		65
SAT	1	2		35		35
CT	2	4	23	60		83
RT	2	1		49		49
MP	3	9	246	153	15	414
RS	1	6	20	28		48
KC	2	6	87	148		235
BEC	1	1	8	7		15
GC	1	1	2			2
HC	1	1	5	9		14
NC	2	2	6	53		59
SGP	2	2	25	25		50
BS	2	5	15	74		89
Total	3[a]	28[a]	473	910	15	1398

*OG, Olrolg's gull; KG, kelp gull; DG, dolphin gull; SAT, South American tern; CT, cayenne tern; RT, royal tern; MP, Magellanic penguin; RS, rock shag; KC, king cormorant; BEC, blue-eyed cormorant; GC, guanay cormorant; HC, hybrid cormorants; NC, neotropic cormorant; SGP, southern giant petrel; BS, brown skua. Nomenclature from del Hoyo *et al.* (1992). †One-year-old individuals. [a]Total number of seasons and different colonies sampled.

Malacalza, Bertelloti & Poretti 1997; Gosztonyi & Kuba 1998; Bertelloti & Yorio 1999; González-Solís, Croxall & Wood 2000; Delhey, Carrete & Martínez 2001; Votier *et al.* 2003), representative prey species were sampled in a manner that maximized variance according to location across colonies and throughout our study area (Table 2). These samples were obtained within seabird foraging areas, inshore and on the shelf up to 200 km offshore, the latter supplied by the fishing industry. Additionally, prey were taken from regurgitates that occurred as we handled the birds. Species determination of prey was conducted directly in the field, as most samples were whole animals. We preserved a small portion of soft tissue from each prey in 5 mL of 70% ethanol for analyses of stable isotopes (Hobson, Gibbs & Gloutney 1997).

ISOTOPIC ANALYSES

Ethanol was removed from prey and blood samples by decanting off excess material, rinsing in distilled water, freeze-drying, and then powdering in a small dental

Table 2. Stable isotope values of carbon and nitrogen (mean ± SE and ranges) and estimated trophic level for components of the Argentinean seabird community and their main prey

Sample	*n*	$\delta^{13}C$ (‰) mean ± SE	$\delta^{13}C$ (‰) range	$\delta^{15}N$(‰) mean ± SE	$\delta^{15}N$(‰) range	Mean trophic level
Invertebrates						
Annelids						
Polychaeta						
Eunice argentinensis	4*	–16·6 ± 0·3	–17·1–16·3	16·6 ± 0·3	15·8–17·1	3·3
Cnidarians						
Anthozoa	3	–14·2 ± 0·3	–14·8–13·2	17·1 ± 0·3	16·8–17·6	3·4
Crustaceans						
Amphipoda	5*	–13·1 ± 0·3	–13·8–12·1	10·2 ± 0·8	7·3–12·2	1·3
Balanus glandula	5*	–15·8 ± 0·2	–16·3–15·1	14·6 ± 0·4	13·2–15·3	2·7
Cyrtograpsus angulatus	8*	–10·8 ± 0·3	–12·1– 9·3	15·2 ± 1·1	10·2–18·1	2·8
Pleoticus muelleri	7	–15·6 ± 0·1	–16·1–15·2	15·4 ± 0·4	14·3–16·6	2·9
Artemesia longinaris	34*	–15·1 ± 0·2	–17·1–13·1	16·1 ± 0·2	14·1–17·5	3·1
Echinoderms						
Asteroidea	5*	–14·3 ± 0·3	–15·4–13·4	14·7 ± 0·2	14·2–15·6	2·7
Molluscs						
Gastropoda						
Trophon geversianus	3*	–14·7 ± 0·1	–14·8–14·6	14·4 ± 0·2	14·0–14·8	2·6
Fisurella spp.	4*	–13·9 ± 0·2	–14·5–13·5	15·0 ± 0·8	13·5–16·7	2·8
Tegula patagonica	2	–12·2 ± 0·7	–12·9–11·5	16·3 ± 0·4	15·9–16·7	3·2
Buccinanops globulosum	2*	–13·5 ± 0·4	–13·9–13·1	16·9 ± 0·5	16·4–17·5	3·4
Patella spp.	5*	–13·9 ± 1·5	–16·7–10·3	13·7 ± 1·9	11·9–16·1	3·6
Polyplacophora	3*	–10·3 ± 1·3	–12·1–7·8	14·4 ± 0·8	13·3–15·7	2·6
Bivalvia						
Mytilus edulis	1*	–14·43		12·32		2·0
Brachidontes rodriguezi	6*	–16·4 ± 0·2	–17·1–15·7	12·8 ± 0·4	11·9–14·6	2·1
Peromytilus purpuratus	5	–16·0 ± 0·4	–17·0–14·8	14·0 ± 0·5	13·0–15·3	2·5
Cephalopoda						
Loligo and *Illex* spp.	17	–17·0 ± 0·5	–21·0–15·1	16·3 ± 0·5	12·3–18·3	3·2
Octopus spp.	4	–12·5 ± 1·0	–15·5–11·3	17·8 ± 0·4	17·5–18·9	3·6
Fish						
Macruronus magellanicus	3	–17·4 ± 0·1	–17·5–17·3	16·2 ± 0·2	15·8–16·5	3·1
Odonthestes incise	10	–16·3 ± 0·3	–17·4–14·4	16·5 ± 0·4	13·5–18·0	3·2
Engraulis anchoita	18	–17·7 ± 0·1	–19·0–16·9	16·4 ± 0·1	14·8–17·3	3·2
Salilota australis	3	–15·6 ± 0·2	–15·9–15·4	16·6 ± 0·1	16·5–16·7	3·3
Merluccius hubbsi	9	–16·5 ± 0·4	–17·5–14·7	17·5 ± 0·4	15·7–19·6	3·5
Callorhynchus callorhynchus	1	–15·0		17·7		3·6
Riveiroclinus eigenmani	8	–16·7 ± 0·2	–17·7–15·8	17·9 ± 0·2	17·1–18·7	3·7
Genypterus blacodes	5	–15·4 ± 0·7	–16·7–13·7	18·0 ± 0·2	17·2–18·6	3·7
Odonthestes smitty	13	–15·2 ± 0·2	–16·1–13·7	18·1 ± 0·2	16·6–18·9	3·7
Eleginops maclovinus	4	–15·4 ± 0·7	–16·9–13·4	18·2 ± 0·5	16·9–19·0	3·8
Seriolella porosa	1	–17·8		18·32		3·8
Raneya fluminensis	7	–15·2 ± 0·4	–16·4–13·5	18·7 ± 0·1	18·2–19·2	3·9
Pseudopercis semifasciata	4	–14·7 ± 0·4	–15·2–13·5	19·5 ± 0·2	18·9–19·8	4·1
Acanthistius brasilianus	4	–15·5 ± 0·3	–16·0–14·6	20·4 ± 0·1	20·2–20·5	4·4
Sea lion excrement	2	–15·5 ± 0·2	–15·7–15·2	19·5 ± 0·0	19·4–19·6	4·1
Seabirds						
Larus atlanticus	11	–12·6 ± 0·4	–15·7–11·3	16·5 ± 0·3	14·7–19·4	3·2
Larus dominicanus	229	–17·5 ± 0·1	–20·7–13·6	18·1 ± 0·1	13·2–20·3	3·8
Sterna hirundinacea	35	–16·8 ± 0·0	–17·4–16·4	18·3 ± 0·1	17·1–19·0	3·8
Thalasseus sandwichensis eurygnatha	83	–16·8 ± 0·0	–16·0–17·5	18·4 ± 0·1	16·6–19·5	3·9
Thalasseus maximus	49	–16·8 ± 0·1	–17·5–16·0	18·7 ± 0·0	18·3–19·2	4·0
Spheniscus magellanicus	414	–16·7 ± 0·0	–18·6–14·8	18·8 ± 0·0	14·1–19·9	4·0
Catharacta antarctica	89	–16·8 ± 0·5	–19·2–15·7	19·0 ± 0·0	18·2–20·4	4·1
Phalacrocorax bougainvillii	2	–16·5 ± 0·0	–16·5–16·5	19·1 ± 0·1	19·0–19·2	4·1
Phalacrocorax magellanicus	48	–16·3 ± 0·1	–17·9–14·8	19·3 ± 0·1	17·6–21·5	4·1
Phalacrocorax atriceps albiventer	236	–16·2 ± 0·0	–17·8–14·6	19·4 ± 0·1	15·1–20·9	4·2
Macronectes giganteus	50	–17·0 ± 0·1	–18·0–16·3	19·4 ± 0·1	18·1–21·0	4·2
P. a. albiventer × *P.a. atriceps* × *P. bougainvillii*	14	–16·6 ± 0·1	–17·0–16·3	19·7 ± 0·1	19·0–20·3	4·3
Phalacrocorax olivaceus	59	–16·1 ± 0·1	–17·0–15·3	20·2 ± 0·1	18·7–21·3	4·4
Phalacrocorax atriceps atriceps	15	–16·3 ± 0·1	–16·7–15·9	20·0 ± 0·1	19·4–20·6	4·4
Leucophaeus scoresbii	65	–15·3 ± 0·1	–17·1–14·2	20·5 ± 0·1	17·4–22·2	4·6

*Samples composed of multiple individuals.

amalgam mill. This technique has been shown to have negligible effect on the stable-carbon and nitrogen isotope values of a variety of tissues (Hobson, Gibbs & Gloutney 1997). Lipids were extracted from prey tissues using a 2 : 1 chloroform : methanol solvent rinse and then dried at 60 °C for 24 h to remove any residual solvent. Extraction of lipids was deemed not necessary for blood samples because the lipid component in blood is generally low (Deuel 1955). Stable-carbon and nitrogen isotope assays were performed on 1 mg subsamples of homogenized materials by loading into tin cups and combusting at 1800 °C in a Europa ANCA-GST elemental analyser (Europa Scientific, Crewe, UK). Resultant CO_2 and N_2 gases were then analysed using an interfaced Europa 20 : 20 continuous-flow isotope ratio mass spectrometer (Europa Scientific) with every five unknowns separated by two laboratory standards (egg albumen). Stable isotope abundance was expressed in standard δ notation relative to carbonate Pee Dee Belemnite and atmospheric nitrogen:

$$\delta^{15}N \text{ or } \delta^{13}C = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \qquad \text{(eqn 1)}$$

where $R = (^{13}C/^{12}C$ or $^{15}N/^{14}N)$, of the sample and standards, respectively. Based on hundreds of measurements of organic standards (albumen and collagen) the analytical precision (± 1 SD) of these measurements is estimated to be ±0·1‰ and ±0·3‰ for carbon and nitrogen, respectively.

ISOTOPIC MODELS

$\delta^{15}N$ values were used for estimating seabird trophic positions. Trophic discrimination between diet and consumer derives from a combination of isotopic discrimination both during assimilation and protein synthesis, and during the excretion of endogenous nitrogen (Ponsard & Averbuch 1999). Although estimates of trophic position are sensitive to the assumption of the trophic fractionation associated with $\delta^{15}N$ values, Post (2002) demonstrated recently that when applied to entire food webs with multiple pathways and many species as studied here, mean described trophic fractionation values is a robust and widely applicable assumption.

To estimate seabird trophic level (TL_{bird}) we assigned the anchovy [*Engraulis anchoita* (Hubbs et Marini)] a trophic level of 3·2 based on a review of its feeding ecology and that of similar primarily herbivorous zooplankton feeding (i.e. TL 3·0) species (Sanger 1987; Tudela & Palomera 1997) and used a $\delta^{15}N_{\text{diet-blood}}$ isotopic fractionation factor between bird blood and lipid-free fish prey of 2·95 (‰). This value is an average of the experimentally derived values of 3·1‰ (Hobson & Clark 1993) and 2·8‰ (Bearhop *et al.* 2002). Thus, a bird feeding exclusively on anchovy would occupy a trophic level of 4·2 and in general:

$$TL_{\text{bird}} = 4{\cdot}2 + [\delta^{15}N_{\text{blood}} - (\delta^{15}N_{\text{anchovy}} + 2{\cdot}95)]/2{\cdot}95 \qquad \text{(eqn 2)}$$

where $\delta^{15}N_{\text{blood}}$ = isotopic signature in the blood of the seabird and $\delta^{15}N_{\text{anchovy}}$ that of anchovy. For all non-avian components of the marine food web, we modified this relationship slightly to reflect whole body or muscle (vs. blood) isotopic fractionation that was expected to be typical of this southern hemisphere temperate food web (3·3‰, Rau *et al.* 1992). Thus, eqn 2 becomes:

$$TL_C = 4{\cdot}2 + [\delta^{15}N_C - (\delta^{15}N_{\text{anchovy}} + 3{\cdot}3)]/3{\cdot}3 \qquad \text{(eqn 3)}$$

where TL_C and $\delta^{15}N_C$ are the trophic level and the isotopic signature in the whole body or muscle of the consumer, respectively (Table 2).

The Argentinean Patagonia community was compared with other seabird communities where stable isotope and trophic level information have been published (Hobson & Welch 1992; Hobson *et al.* 1994; Sydeman *et al.* 1997; Hobson *et al.* 2002). In addition, TLs were calculated for two more studies where only stable isotopes of nitrogen were measured (Rau *et al.* 1992; Thompson *et al.* 1999).

Thompson *et al.* (1999) provided information about the $\delta^{15}N$ values in the liver of six species of Iceland seabirds and their prey, including capelin [*Mallotus villosus* (Müller)], one of the most consumed foods in the study area. Sanger (1987) places capelin at TL of 3·2. Using this value and a trophic enrichment factor of 2·7‰ for liver of seabirds (Hobson & Clark 1992) leads to the following TL derivation:

$$TL_{\text{bird}} = 4{\cdot}2 + [\delta^{15}N_{\text{liver}} - (\delta^{15}N_{\text{capelin}} + 2{\cdot}7)]/2{\cdot}7 \text{ or}$$

$$TL_{\text{bird}} = 4{\cdot}2 + (\delta^{15}N_{\text{liver}} - 13{\cdot}5)/2{\cdot}7 \qquad \text{(eqn 4)}$$

Following Hodum & Hobson (2000), Antarctic krill was assigned a TL of 2·3. Rau *et al.* (1992) used muscle samples of seabirds and so we used a fractionation factor of 3·3‰ for calculating TL of Weddell Sea seabirds:

$$TL_{\text{bird}} = 4{\cdot}2 + [\delta^{15}N_{\text{muscle}} - (\delta^{15}N_{\text{krill}} + 3{\cdot}3)]/3{\cdot}3 \text{ or}$$

$$TL_{\text{bird}} = 4{\cdot}2 + (\delta^{15}N_{\text{muscle}} - 5{\cdot}6)/3{\cdot}3 \qquad \text{(eqn 5)}$$

Values of stable isotopes are presented as mean ± SE. Comparisons among species were performed using ANOVA, and when significant results were obtained we made *post hoc* comparisons with Tukey's test. The $\delta^{15}N$ and $\delta^{13}C$ values were also compared simultaneously using a multivariate analysis of variance (MANOVA) with the Wilks's lambda statistic. For comparisons within groups of phylogenetically related species (cormorants, terns and gulls), only the isotope values of chicks were analysed, as this age category was well sampled across all species.

Results

COMPARISON OF SEABIRD COMMUNITIES

Our model for calculating trophic level predicted that 13 of 14 (93%) seabirds in Patagonia were within a range

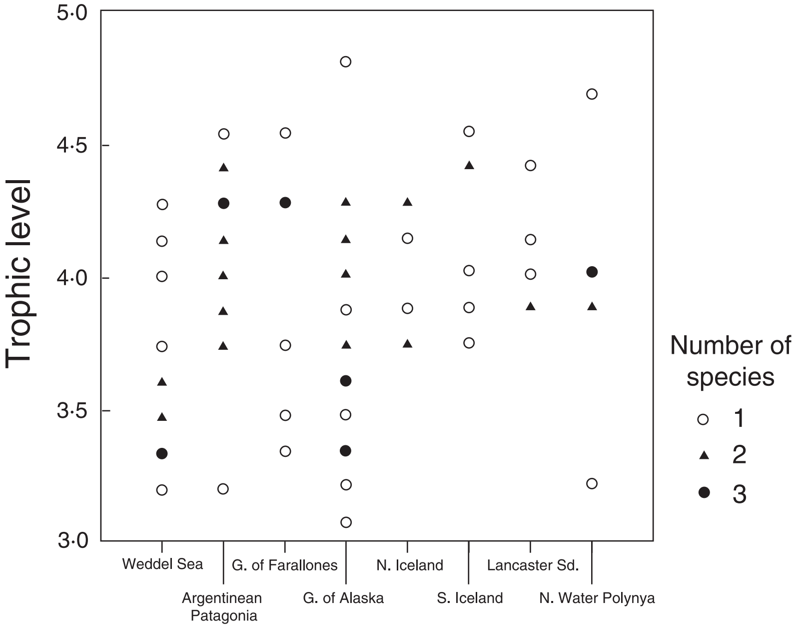

Fig. 2. Comparison of mean trophic level per species within different seabird communities.

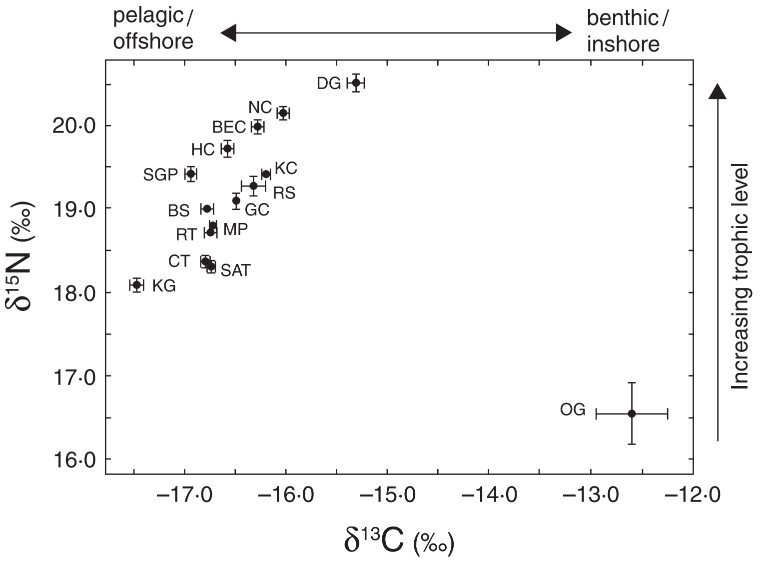

Fig. 3. Mean ± SE stable-carbon and nitrogen isotope concentrations in blood of seabirds from the Chubut coast. Species codes according to Table 1.

of 0·7 trophic levels, which is narrower than in other communities with a similar number of species (Fig. 2). The community of Argentinean Patagonia also showed a higher degree of overlap in trophic level than in other localities (Fig. 2): the coefficient of variation (CV) was low (7·9) compared to other communities with a similar (Weddell Sea, Antarctica, 12 species, CV = 8·9; Rau *et al.* 1992) or even higher number of species (Gulf of Alaska, 19 species, CV = 11·4; Hobson *et al.* 1994). Seabirds in Argentina showed a higher mean trophic level than the communities of the Weddell Sea and Gulf of Alaska (4·1 vs. 3·6 and 3·7; $F_{2,45} = 4·7$, $P = 0·01$, Tukey's test, $P = 0·01$ and $P = 0·06$, respectively).

PATAGONIAN SEABIRD TROPHIC RELATIONSHIPS

Stable isotope values for seabirds are presented in Table 2 and Fig. 3. Despite the narrow range in isotope values (Fig. 2), overall there was a significant effect of species on isotope signatures (MANOVA: Wilks's lambda = 0·34, $F_{28,2766} = 79·2$, $P < 0·0001$). Stable-nitrogen isotopes for seabirds were correlated positively with $\delta^{13}C$ values (Pearson correlation, $r = 0·44$, $n = 1398$, $P < 0·0001$). Extremes in isotope values were shown by the three gull species (Fig. 3). Olrolg's gull showed the lowest and highest values of $\delta^{15}N$ and $\delta^{13}C$, respectively. The

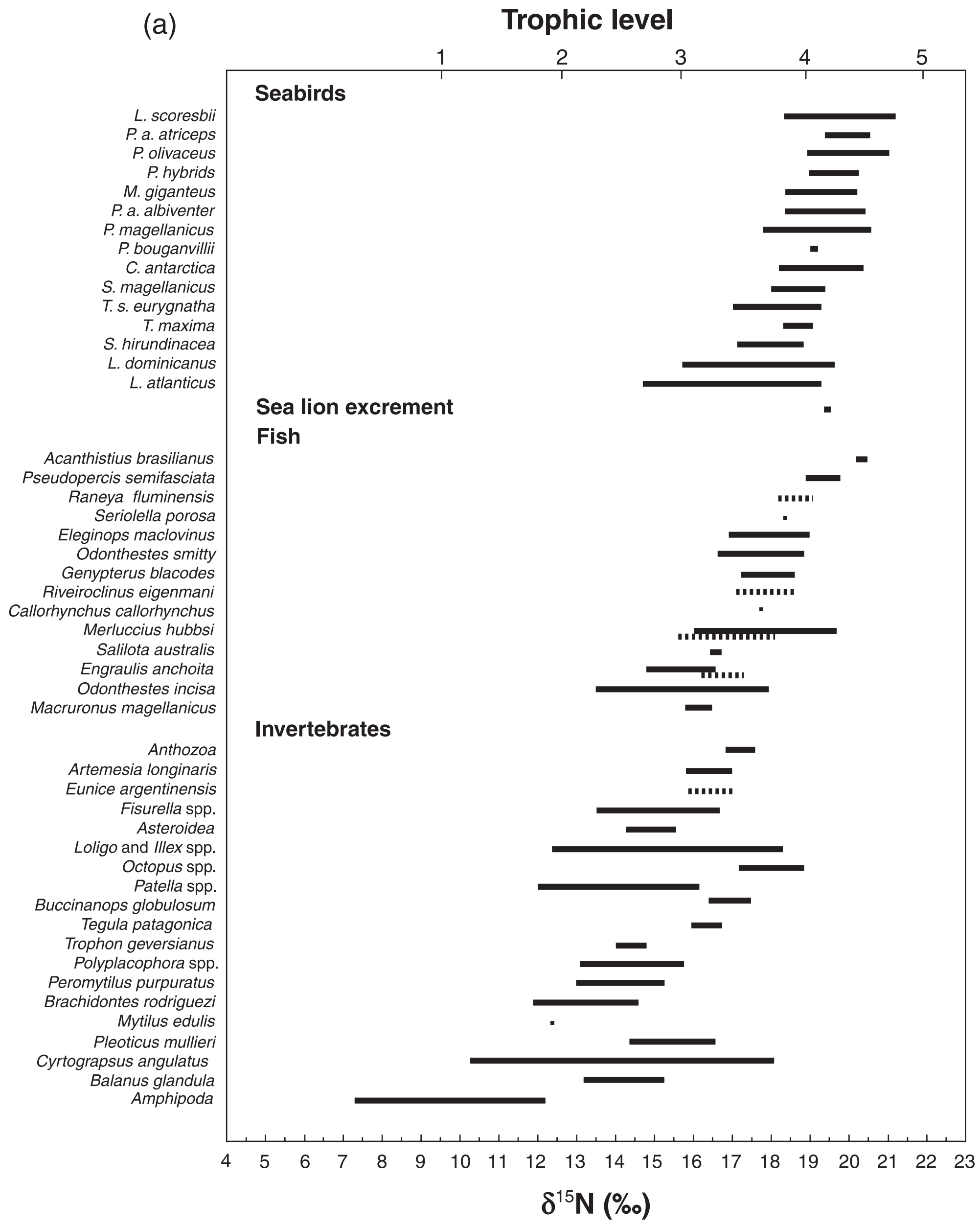

Fig. 4. Stable nitrogen (a) and carbon (b) isotope concentrations (5–95% percentiles) and trophic levels of main components of the marine food web in the Chubut province. Spotted lines indicate the values for prey obtained by regurgitation of seabirds. Stable isotope signatures of regurgitates did not differ significantly from the values of the same prey species obtained by other sampling modes (MANOVA, $F_{4,120} = 0{\cdot}296$, $P = 0{\cdot}88$).

dolphin gull [*Leucophaeus scoresbii* (Traill)] was the most enriched in ^{15}N and kelp gull showed the most depletion in ^{13}C.

FOOD WEB

There was a significant effect of taxonomic group on the combined stable isotope signatures of prey (MANOVA: Wilks's lambda = 0·07, $F_{66,360} = 14{\cdot}6$, $P < 0{\cdot}0001$). Stable nitrogen isotope signatures (mean ± SE) of prey ranged from 10·2 ± 0·8‰ in amphipods to 20·4 ± 0·1‰ in Argentine sea bass [*Acanthistius brasilianus* (Cuvier)] (Table 2, Fig. 4a). Chitons (Polyplacophora) and crabs [*Cryptograspus angulatus* (Dana)] showed the highest mean values of carbon isotope signatures. Silver warehou [*Seriolella porosa* (Guichenot)] and anchovy had the lowest mean δ^{13}C signatures (Table 2, Fig. 4b).

The different categories of primary seabird prey were segregated isotopically (MANOVA: Wilks's lambda = 0·22, $F_{14,300} = 24{\cdot}3$, $P < 0{\cdot}0001$) (Fig. 5). Relative positions of seabirds and prey indicated that seabirds have diets composed mainly of fish, and to lesser degree invertebrates, with the exception of Olrolg's and dolphin gulls that seem to be more specialist feeders (Fig. 5). Crabs, the main prey of Olrolg's gull (Delhey *et al*. 2001), showed lowest δ^{15}N values and highest δ^{13}C values, respectively, being statistically different from octopus, benthic and pelagic fish and sea lion excrement in δ^{15}N values (Tukey's

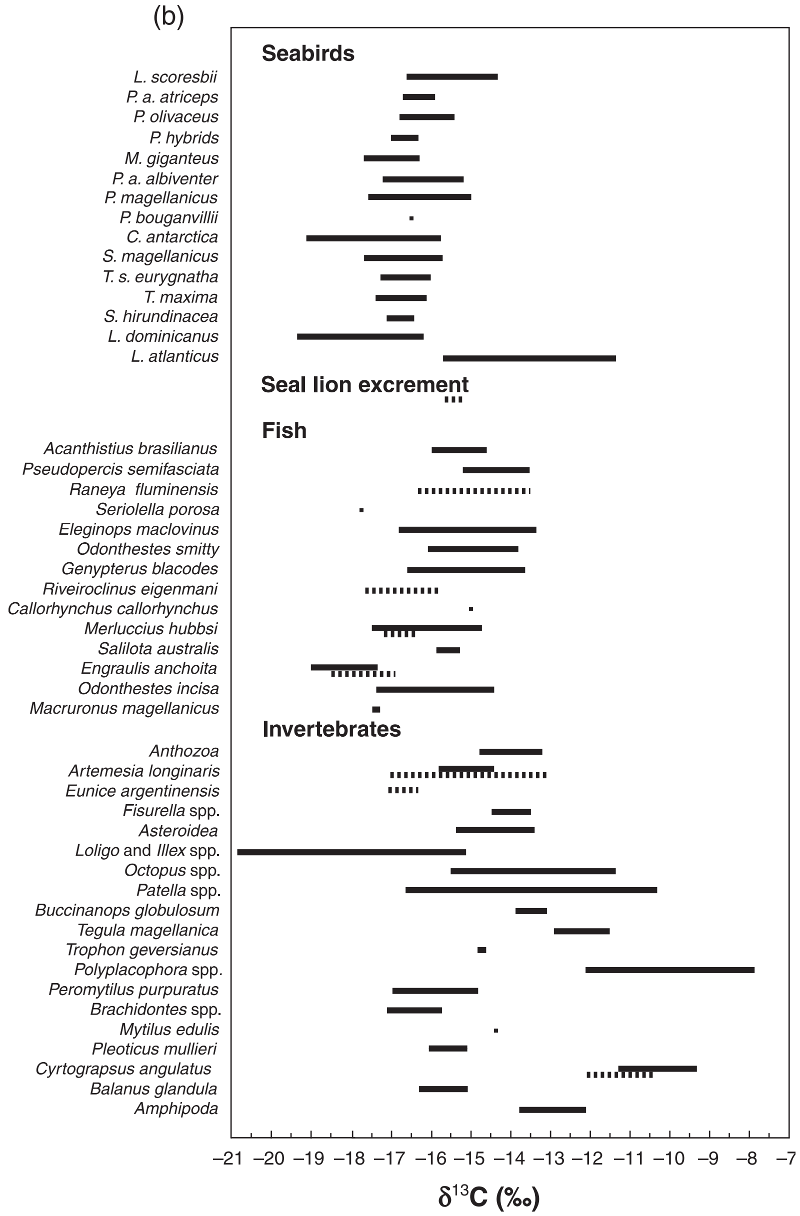

Fig. 4. *Continued*

test, all $P < 0{\cdot}04$). Stable-carbon isotope values of crabs differed significantly from all prey species (all $P < 0{\cdot}0001$) except octopus ($P = 0{\cdot}35$). The two groups of cephalopods, octopus and squids, differed in their carbon isotope signatures ($P < 0{\cdot}001$) but showed similar δ^{15}N values ($P = 0{\cdot}52$). Benthic and pelagic fish differed in both their δ^{15}N values ($P < 0{\cdot}0001$) and δ^{13}C values ($P = 0{\cdot}004$).

OVERLAP AMONG RELATED SPECIES

Gulls showed the largest (3·2–4·6), cormorants intermediate (4·1–4·4) and terns the narrowest (3·8–4·0) range in trophic level (Table 2, Fig. 4a). The three gull species were segregated isotopically (Wilks's lambda = 0·17, $F_{4,574} = 204{\cdot}6$, $P < 0{\cdot}0001$) differing both in their δ^{15}N (ANOVA: $F_{2,290} = 174{\cdot}5$, $P < 0{\cdot}0001$, Tukey's test, all $P < 0{\cdot}0001$) and δ^{13}C values ($F_{2,290} = 209{\cdot}5$, $P < 0{\cdot}0001$, Tukey's test, all $P < 0{\cdot}0001$) (Fig. 6a).

Although chicks of four species of cormorants and also hybrids statistically segregated in isotope signatures (Wilks's lambda = 0·74, $F_{8,478} = 9{\cdot}82$, $P < 0{\cdot}0001$), there was considerable overlap among species (Fig. 6b). Differences among species were significant for each isotope (δ^{15}N: $F_{4,244} = 19{\cdot}29$, $P < 0{\cdot}0001$; δ^{13}C: $F_{4,244} = 3{\cdot}62$, $P = 0{\cdot}007$). Nitrogen effectively segregated the neotropic cormorant [*P. olivaceus* (Humbolt)] from rock shag [*P. magellanicus* (Gmelin)] (Tukey's test, $P < 0{\cdot}0001$) and king cormorant (Tukey's test, $P < 0{\cdot}0001$). Overlap in carbon isotope values was higher, and only neotropic and king cormorants were separated by these values (Tukey's test, $P = 0{\cdot}007$) (Fig. 6b). Isotope values from hybrid chicks were enclosed within the distributions of values of the parental species.

Overall, tern species were segregated isotopically (Wilks's lambda = 0·84, $F_{4,280} = 6{\cdot}3$, $P < 0{\cdot}0001$); however, when we analysed isotopes separately, species

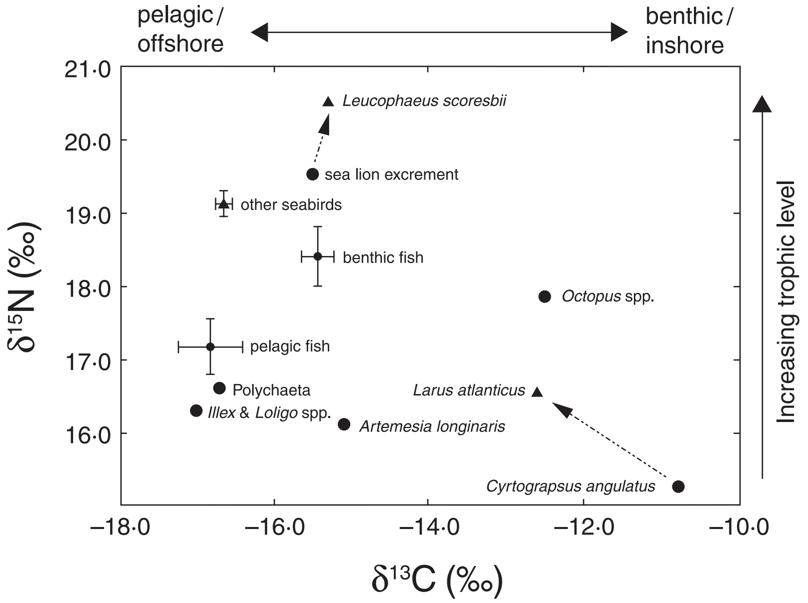

Fig. 5. Stable-carbon and nitrogen isotope concentrations of the seabirds and their main prey. Arrows connect the most specialist predators in the community with their main prey. Means are mean values by species (± SE).

segregated according to δ^{15}N ($F_{2,143} = 12{\cdot}7$, $P < 0{\cdot}0001$) but not δ^{13}C ($F_{2,143} = 0{\cdot}03$, $P = 0{\cdot}97$) values. Cayenne [*Thalasseus sandwichensis* (Latham)] and royal terns [*T. maximus* (Boddaert)] had similar δ^{15}N values (Tukey's test, $P = 0{\cdot}88$) and higher ones than the South American tern (*Sterna hirundinacea* Lesson) ($P_s < 0{\cdot}0001$) (Fig. 6c).

Discussion

Overall, the marine food web showed stable-carbon and nitrogen isotopic enrichment with trophic level. That permitted a dual isotope approach to evaluating trophic structure and source of feeding. The range in δ^{15}N values of seabirds and prey revealed a food web characterized approximately by five trophic levels (Fig. 4a) similar to those in both northern (Hobson & Welch 1992; Sydeman *et al.* 1997) and southern oceans (Wada *et al.* 1987; Rau *et al.* 1992; Dunton 2001).

No calculation of trophic levels has been previously established for the seabird community in Argentinean Patagonia. Available information on diet for some of the species agrees with the importance of fish as a primary food resource in the community (Malacalza *et al.* 1994, 1997; Gosztonyi & Kuba 1998). Analyses of food samples revealed that Olrolg's (TL = 3·2) and dolphin gulls (TL = 4·6) were 0·4 TL above crabs (TL = 2·8) and 0·5 above sea lion excrement (TL = 4·1), respectively. This suggests a broader diet than known previously (Yorio *et al.* 1996; Delhey *et al.* 2001), including a substantial proportion of prey at lower trophic levels. Similarly, our results for the southern giant petrel were unexpected given previous literature. The giant petrel is the largest avian predator–scavenger in the Patagonian seabird community but it showed lower δ^{15}N values than would occur on a diet based primarily on penguin carrion as suggested elsewhere (Hunter & de Brooke 1992; González-Solís *et al.* 2000). Although we too observed avian predation and scavenging on birds and seals, the derived TL value of petrels suggests a mixed diet, probably including a high proportion of crustaceans, cephalopods and fish.

Stable-carbon isotope values of seabirds were largely in concordance with expectation from the literature. Species with highest δ^{13}C values, indicating inshore foraging, were dolphin and Olrolg's gulls (Figs 3 and 4a). Species known to be pelagic, such as the southern giant petrel (González-Solís *et al.* 2000), showed lower δ^{13}C value. However, the kelp gull [*Larus dominicanus* (Lichtenstein)] exhibited a more negative mean δ^{13}C value than the southern giant petrel (Table 2, Fig. 3). This result could be explained, at least partially by kleptoparasitic behaviour and also by the use of human fishery discards (primary pelagic fish) by this gull (Bertelloti & Yorio 1999).

Despite differences in body size and morphological adaptations for feeding, 93% of Patagonian seabird species were within a range of only 0·7 trophic levels. When compared to other communities, these seabirds occupied a relatively narrow and high trophic level. In our study, only one of 15 species (considering hybrid cormorants) (7% of the community) was at a TL < 3·8. In contrast, nine of 19 species (47%) in the Gulf of Alaska (Hobson *et al.* 1994) and eight of 12 (67%) in the Weddell Sea were below that level (Rau *et al.* 1992).

Considering groups of phylogenetically related species, we predicted that there should be minimal dietary overlap in sympatric species that are morphologically similar. Such a prediction was true for gulls (Fig. 6a), but all five species of cormorants showed a higher degree of overlap in their stable isotope values (Fig. 6b). The most distinct member of the latter group was the neotropic cormorant, a species with the largest breeding distribution on the coast and inland along rivers and lakes (del Hoyo, Elliott & Sargatal 1992). This segregation, however, was not due to an effect of inland breeders, as all colonies sampled in our study were located along the coast where birds foraged exclusively in marine areas. The wide range of $\delta^{13}C$ values found in the rock shag agrees with a diet composed of benthic and pelagic fish, and polychaetes (Malacalza *et al.* 1997). Among tern species the overlap was especially high for $\delta^{13}C$ values, demonstrating that they feed on prey occurring in similar marine zones. Royal and cayenne terns fed at similar trophic levels, while South American terns fed at a lower trophic level. The South American tern is the smallest of the three species, and this may suggest a diet of species or individuals of smaller size. It is interesting to note that this segregation parallels the aggregation in breeding colonies in the Argentinean Patagonia. Cayenne and royal terns breed together at high densities, or in less dense colonies associated with the South American tern, while the latter often appears where the other two species are not present (Quintana & Yorio 1997). The fact that there was some overlap even among gull species (Fig. 6a), i.e. the species with extreme mean isotope values (Fig. 3), emphasizes the considerable degree of overlap among all seabirds in this community.

Trophic similarity does not necessarily mean dietary similarity because several prey species can occur at the same trophic level. In addition, trophic level estimates using stable isotope methods can provide a misleading impression of trophic overlap as, for example, an individual consuming 50% of its diet at TL 3 and 4, respectively, will have the same TL value (i.e. a mean TL of 3·5) as an individual consuming 100% of its diet at TL 3·5. In this sense, TL derivations are more useful in the context of energy flow or the flux of contaminants or elements through foodwebs (e.g. Hobson *et al.* 2002a) vs. detailed dietary investigations *per se*. None the less, in systems that are characterized by few dietary alternatives at each trophic level, and in particular where seabird diet is often based on a superabundance of a single prey type such as anchovy (Forero *et al.* 2002a), Arctic cod (*Boreogadus saida*, Hobson & Welch 1992) or krill (*Euphausia* sp.; Croxall & Prince 1987) then trophic overlap has a high probability of representing actual dietary overlap. We believe this is the case for the seabird community of Argentinean Patagonia and several other polar and temperate seabird communities we have considered.

Seabird trophic level estimate varies directly with assumed forage fish TL in the model and so error associated with that model variable will affect the seabird TL estimate by the same magnitude. Our assumed anchovy TL of 3·2 was based on literature estimates and predicts that these fish consumed primarily but not exclusively herbivorous zooplankton (i.e. TL 2·0). The extent to which anchovy differ from TL 3·2 will depend on how much primary carnivore zooplankton (i.e. TL 4·0) they consume. A reasonable error to associate with this variable is ±0·2. For the diet-tissue discrimination

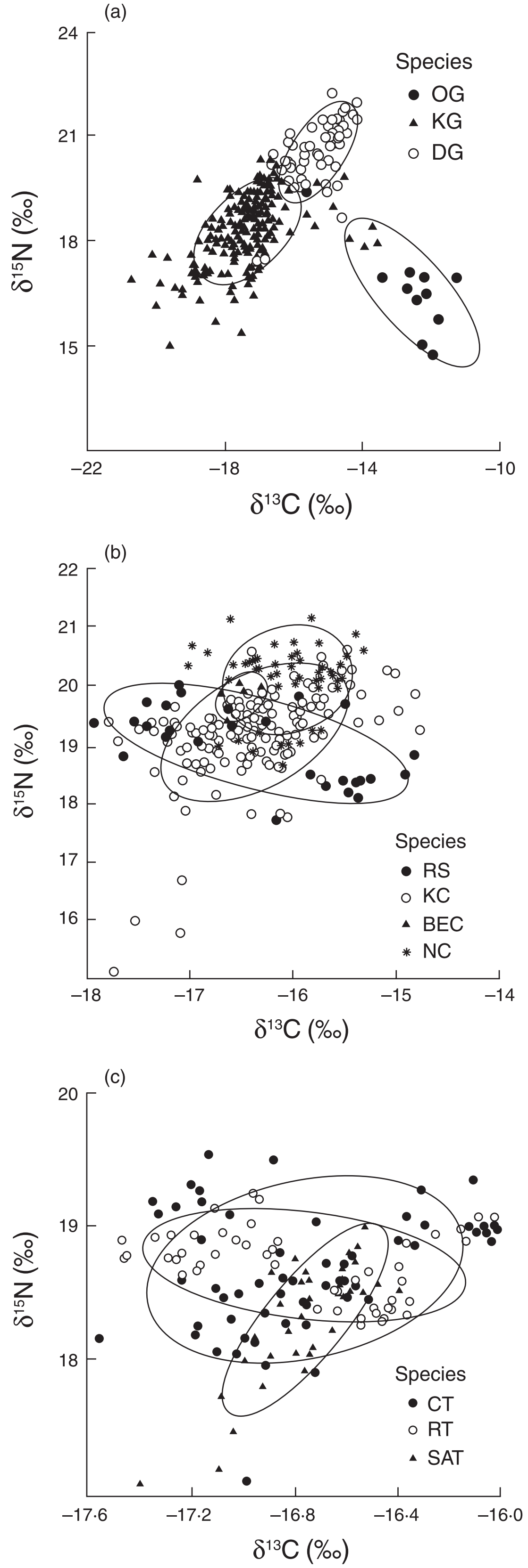

Fig. 6. Stable nitrogen and carbon isotope concentrations of blood of gulls (a), cormorants (b) and terns (c). Hybrid individuals were not represented. We represent the Gaussian bivariate ellipses for the sample in each plot or Gaussian bivariate confidence intervals on the centroid. Species codes according to Table 1.

factor, we were encouraged that the Hobson & Clark (1993) and the Bearhop *et al*. (2002) experimental studies were reasonably close (3·1‰ vs. 2·8‰) and feel that our mean estimate of 2·95‰ to be the best currently available. An assumed error of ±0·2‰ for this variable is not unreasonable. Combining both sources of error results in an overall error estimate for seabird TL of approximately 12%.

If our above assumption of high dietary overlap is true, the question arises how species within the community coexist. The extensive degree of overlap we measured for breeding seabirds may be even more extreme considering that another 40 non-breeding species can be found using the Argentinean continental shelf as a foraging ground (Yorio 2000). Ecological theory predicts that coexistence of potential competitors and the regulation of their populations could be interpreted in part as being a consequence of superabundance of food (Pianka 1976). Even if a superabundance of food resources for seabirds exists in our area and permits coexistence of species, selection could be operating to diversify morphology and foraging strategies. For example, seabird populations can be regulated by the existence of temporal food shortages such as that reported in coastal Peru during the El Niño phenomenon (Ramos *et al*. 2002; Simeone *et al*. 2002), or also conditioned by stochastic processes (Wooller, Bradley & Croxall 1992). Competitive processes may also operate during the non-breeding period when seabird diet is essentially unknown (but see Cherel, Hobson & Weimerskirch 2000).

Our results are not only important from an ecological point of view but also have relevant implications for conservation of these species. The narrow trophic niche of the seabird species in the Argentinean Patagonia and the dependence of a high number of species upon a few prey types (i.e. mainly pelagic fish) make them highly vulnerable to the reduction of fish stocks (Yorio 2000). The comparatively high mean trophic level of this seabird community is also of interest from the perspective of resilience to foodweb fluctuations. Sanger (1987) speculated that the previously unexpected dependence of seabirds in the Gulf of Alaska on lower trophic-level prey such as pelagic invertebrates (as confirmed by the isotopic study of Hobson *et al*. 1994) might be an adaptation to periodic fluctuations in biomass of upper trophic-level prey such as forage fish stocks. These authors speculated that there may be strong selection toward lower trophic level prey in seabird communities occupying particularly stochastic marine environments. Our finding of a relatively high trophic position for the Argentinean Patagonia seabird community suggests either a low frequency of stochastic fluctuations in the system, or may undermine Sanger's (1987) argument if periodic fluctuations are high.

Our study revealed that rather than considering mean isotopic signatures *per se*, examination of isotopic variance within species provides new insights into individual feeding ecology. The perception of the degree of overlap among species was heavily dependent on sample size and how results were presented. Traditionally stable isotope results, usually based on only few individuals, are displayed as mean and standard errors. For our data, there appear to be highly distinct trophic patterns when plotted that way (Fig. 3) and when analysed statistically. However, an extensive amount of overlap was effectively hidden. By plotting individual values (Fig. 6) a more meaningful view of intra- and interspecific trophic ecology emerges.

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