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### Trophic niche overlap between sympatric resident and transient populations of bottlenose dolphins in the Humboldt Current System off north-central Chile

MACARENA SANTOS-CARVALLO,<sup>1</sup> Centro de Investigación y Gestión en Recursos Naturales (CIGREN), Instituto de Biología, Facultad de Ciencias, Universidad de Valparaíso, Av. Gran Bretaña 1111, Playa Ancha, Valparaíso, Chile and Centro de Investigación Eutropia, Ahumada 131 Oficina 912, Santiago, Chile; **MARÍA JOSÉ PÉREZ-ÁLVAREZ**, Centro de Investigación Eutropia, Ahumada 131 Oficina 912, Santiago, Chile and Instituto de Ecología y Biodiversidad (IEB), Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile; **VERÓNICA MUNIAIN**, Centro de Investigación y Gestión en Recursos Naturales (CIGREN), Instituto de Biología, Facultad de Ciencias, Universidad de Valparaíso, Av. Gran Bretaña 1111, Playa Ancha, Valparaíso, Chile; **RODRIGO MORAGA**, Centro de Investigación Eutropia, Ahumada 131 Oficina 912, Santiago, Chile; **DORIS OLIVA**, Centro de Investigación y Gestión en Recursos Naturales (CIGREN), Instituto de Biología, Facultad de Ciencias, Universidad de Valparaíso, Av. Gran Bretaña 1111, Playa Ancha, Valparaíso, Chile; **MARITZA SEPÚLVEDA**, Centro de Investigación y Gestión en Recursos Naturales (CIGREN), Instituto de Biología, Facultad de Ciencias, Universidad de Valparaíso, Av. Gran Bretaña 1111, Playa Ancha, Valparaíso, Chile and Centro de Investigación Eutropia, Ahumada 131 Oficina 912, Santiago, Chile.

The ecological niche refers to the biotic and abiotic conditions in which a species lives, including its temporal variations (Hutchinson 1957, Pianka 1978). However, the niche concept has remained elusive because there are different concepts that emphasize different aspects of a species' ecological characteristics (Leibold 1995). Despite the many different concepts, all contemporary definitions retain the formalization of niche as an  $n$ -dimensional space (Newsome *et al.* 2007).

In recent years the use of stable isotope ratios has allowed isotopic ecologists to quantify niche dimensions using the concept of "isotopic niche" (Newsome *et al.* 2007). The isotopic niche is defined as an area (in  $\delta$ -space) with isotopic values ( $\delta$ -values) as coordinates. This " $\delta$ -space" (for example  $\delta^{13}\text{C}$  *vs.*  $\delta^{15}\text{N}$  biplot) is comparable

<sup>1</sup>Corresponding author (e-mail: msantos@eutropia.cl).

to the  $n$ -dimensional space that contains what ecologists refer to as the ecological niche, since an animal's chemical composition is directly influenced by what it consumes as well as the habitat in which it lives (Newsome *et al.* 2007). Ratios of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopes are usually used to quantify isotopic niche because the values of these isotopes in the consumer tissues are closely linked to those in their diet (Layman *et al.* 2007). Ratios of carbon are generally used to evaluate foraging habitats, whereas ratios of nitrogen isotopes are used to quantify the relative position of a consumer in a trophic web (DeNiro and Epstein 1978).

Insights into the isotopic niche can also be gained with the use of metrics to calculate community-wide measures of trophic structure using  $\delta^{13}\text{C}$  vs.  $\delta^{15}\text{N}$  biplot with individuals, populations, or species plotted in this niche space based on their mean stable isotope signatures (Layman *et al.* 2007, Jackson *et al.* 2011). The trophic niche and its relative position can be analyzed using quantitative metrics that reflect relevant aspects of trophic structure within a food web (Layman *et al.* 2007). Thus community-wide metrics provide a framework to investigate ecology from individuals to communities, allowing assessment of trophic relationships and feeding niche (*e.g.*, Jaeger *et al.* 2013), dietary variation in space and/or time (*e.g.*, Mendes *et al.* 2007), and resource partitioning or niche overlap within and between species (*e.g.*, Browing *et al.* 2014).

The bottlenose dolphin, *Tursiops truncatus*, has a cosmopolitan distribution and inhabits both coastal and oceanic habitats of temperate and tropical waters (Wells and Scott 2009). This species exhibits a wide range of intraspecific variation in several aspects of its behavioral ecology (Gubbins 2002), including ranging patterns, movements, site fidelity, and diet (Wilson *et al.* 1997, Bearzi *et al.* 2009). Some individuals are year-round residents, staying within a small home range (*e.g.*, 15–65 km<sup>2</sup>, Gubbins 2002) and living in the same area for many years or even their entire life (Connor *et al.* 2000). Other dolphins are transient with little or no site fidelity (Defran *et al.* 1999) and larger home ranges (Ballance 1992, Defran and Weller 1999) for instance, 63–725 km<sup>2</sup> (Silva *et al.* 2008). When resident and transient bottlenose dolphins co-occur within the same region, they generally have different feeding and habitat preferences (Wilson *et al.* 1997). These variations of habitat and resource use patterns could be a strategy to reduce intraspecific competition and thus maximize foraging success (Wilson *et al.* 1997).

Differences in diet composition and/or habitat use may be reflected in the way that isotopic niches are structured, as has been reported at interspecific levels for several cetacean species, especially delphinids (*e.g.*, Gross *et al.* 2009, Kiszka *et al.* 2010), but to a lesser extent at the intraspecific level (*e.g.*, Barros *et al.* 2010, Kiszka *et al.* 2012). In the case of the bottlenose dolphin, it has been reported that a differentiation in isotopic niches between sympatric groups could be due to trophic and habitat segregation (Barros *et al.* 2010, Kiszka *et al.* 2012). To our knowledge, however, there are no comparative studies on isotopic niche partitioning among sympatric resident and transient bottlenose dolphins.

In north-central Chile, sympatric resident and transient bottlenose dolphins differing in their behavioral, group size and site fidelity have been described (Thomas 2005, Santos 2013). Resident individuals show a high residence (>15 yr) and a strong site-fidelity using the area for feeding, nursing, and calving. They are usually seen in groups of 15–20 individuals (range 2–40) (Gibbons 1992, Thomas 2005). In contrast, transient bottlenose dolphins show a lower rate of residency and are usually seen in larger group sizes of approximately 70 individuals (range 5–1,000). This group

uses the area mainly as a corridor, and to a lesser degree as a feeding area, since feeding activities have been observed within the area (Santos 2013).

No studies on the trophic ecology and isotopic niche partitioning have been carried out for this species in the area. However, since both resident and transient populations have been seen simultaneously inhabiting the same area, a certain degree of resource partitioning between both groups is expected. Also, because a larger home range in transient bottlenose dolphins has been suggested (Ballance 1992), a broader isotopic niche in this group is predicted. Our goal is to describe the spatial fine-scale trophic structure and the trophic interactions between resident and transient bottlenose dolphins in the Humboldt Current System of north-central Chile through the use of stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope analysis.

The study area is located in two Chilean marine protected areas: Chañaral Island ( $29^{\circ}02'\text{S}$ ,  $71^{\circ}36'\text{W}$ ) and Choros-Damas Island ( $29^{\circ}14'\text{S}$ ,  $71^{\circ}32'\text{W}$ ), hereafter referred to as RMC-CD (Fig. 1). The area is a highly dynamic and productive coastal environment located in one of the most important upwelling focus of the Humboldt Current System (Thiel *et al.* 2007) that allows for the presence of a wide variety of marine predators, including mammals and birds (Luna-Jorquera *et al.* 2003, Pérez *et al.* 2006).

In order to determine whether the individuals analyzed were resident or transient, we used the residence index (RI) using the following equation (modified from Lusseau 2005):

$$RI = \frac{S}{M} \times 100$$

where  $RI$  = residence index,  $S$  = total number of months in which a particular individual was seen, and  $M$  = total number of monthly surveys.

Individual bottlenose dolphins were identified by recognition of their individually distinctive dorsal fins previously classified in a photo-identification catalog (Thomas 2005, Santos 2013). We considered as residents those animals with a  $RI > 30\%$  (Thomas 2005), and that were observed year-round in the RMC-CD; whereas transient dolphins were considered as those animals with a low degree of site fidelity ( $RI < 30\%$ ).

For stable isotopes analysis, we collected skin samples from 38 adult free-ranging individuals, from February 2009 to January 2010 (Table 1). Samples were obtained from a 7-m-long boat using a modified PaxArms .22 caliber rifle and biopsy darts, which allow extraction of a small sample of skin from animals swimming parallel to the boat at a distance of 2–5 m. PaxArms biopsy darts have a hollow bright red polycarbonate body with a plastic tailpiece and a steel biopsy tip that is beveled inwards. The cutting tip has a 5 mm diameter and 9 mm length. The total length of an assembled dart is approximately 140 mm and its total weight is 21.5 g (Krützen *et al.* 2002).

In the laboratory, skin samples (epidermis) were dried in an oven at  $60^{\circ}\text{C}$  for 72 h. Samples were then ground in a porcelain mortar and stored in filter paper. Due to the fact that lipids tend to be depleted in  $^{13}\text{C}$  relative to protein and carbohydrates, they have the potential to influence stable isotope analyses using  $\delta^{13}\text{C}$  (McCutchan *et al.* 2003, Post *et al.* 2007). Therefore, lipids were extracted from samples in a Soxhlet extractor with petroleum ether for 2 h. A  $0.5 (\pm 0.05)$  mg subsample of skin tissue

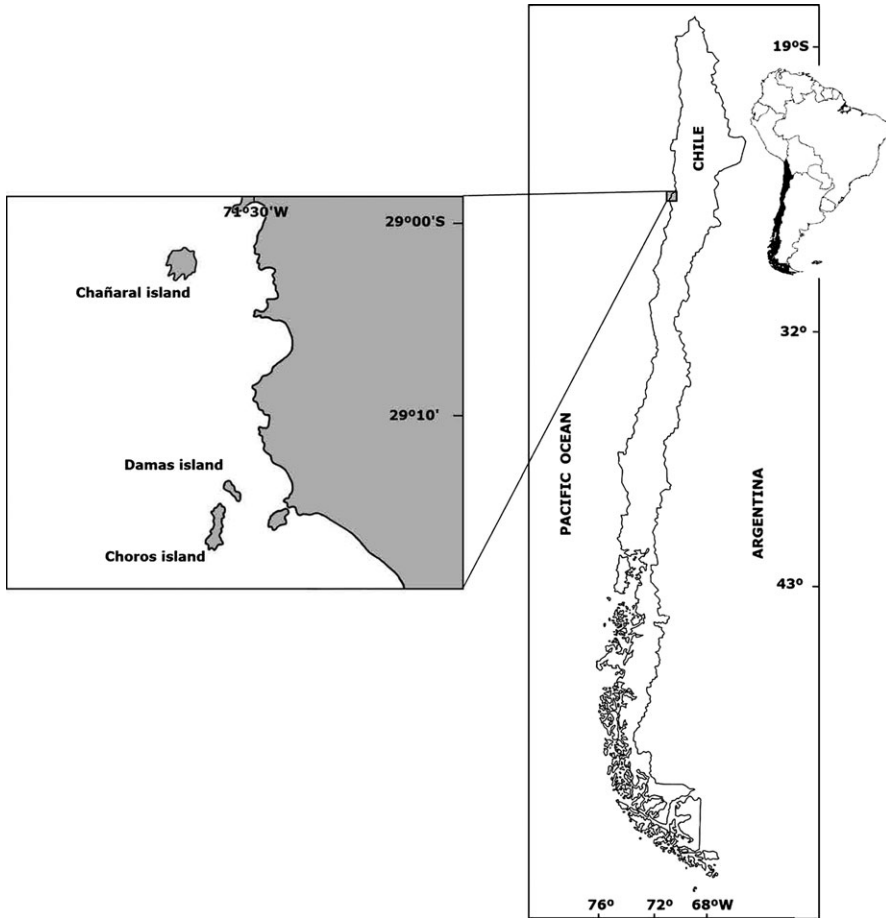


Figure 1. Map of the study area showing the Chañaral Island and Choros-Damas Island Marine Reserves, north-central Chile.

Table 1. Community-wide metrics for resident and transient bottlenose dolphins in north-central Chile: carbon range (CR); nitrogen range (NR); convex hull or total area (TA); and standard ellipse area ( $SEA_C$ ), expressed as the area in trophic space ( $\%_0^2$ ).

Group	<i>n</i>	$\delta^{13}C$		$\delta^{15}N$		CR	NR	TA	$SEA_C$
		Mean	SD	Mean	SD				
Resident	8	-16.0	0.16	20.1	0.33	0.53	0.81	0.24	0.16
Transient	30	-16.0	0.26	20.1	0.56	1.18	2.18	1.62	0.46

was sealed in a tin capsule for stable isotope analysis.  $\delta^{13}C$  and  $\delta^{15}N$  values were determined using a Carlo-ErbaNC 2500 (Milan, Italy) or Costech 4010 (Valencia, CA) elemental analyzer interfaced with a Thermo-Finnigan Delta Plus XL isotope ratio mass spectrometer (Waltham, MA) at the University of Wyoming Stable

Isotope Facility (Laramie, WY). Stable isotope data are expressed in delta notation ( $\delta$ ) as parts per thousand (‰) using the following equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left[ \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right] \times 10^3$$

where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  ratios of the sample and standard, respectively. The standards were Vienna-Pee Dee Belemnite limestone (VPDB) for carbon and atmospheric  $\text{N}_2$  for nitrogen.

Four niche metrics to estimate the trophic niche width of resident and transient bottlenose dolphin were calculated: carbon range (CR), nitrogen range (NR), convex hull or total area (TA) and standard ellipse area corrected for small sample sizes ( $\text{SEA}_C$ ) (Layman *et al.* 2007, Jackson *et al.* 2011). CR, NR, and TA are measures of the total extent of spacing within  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  biplot space, *i.e.*, the community-wide metrics (Layman *et al.* 2007), and  $\text{SEA}_C$  is a measure of the mean core population isotopic niche (Jackson *et al.* 2011). CR was calculated as the distance between the most enriched and the most depleted  $^{13}\text{C}$  values of each bottlenose dolphin group, and it represents the variability of food sources consumed. NR corresponds to the difference between the most enriched and the most depleted  $^{15}\text{N}$  values of each population, and may indicate the capacity of the species or population to consume organisms occupying different trophic levels. TA encompasses all data points for each species or population and represents the overall niche diversity of each species or population along both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  niche dimensions. Finally,  $\text{SEA}_C$  (expressed in ‰<sup>2</sup>; Batschelet 1981) represents the mean core area of each species' or populations' isotopic niche. The subscript "c" indicates that a small sample size correction was used (Jackson and Britton 2014). We also calculated the Bayesian estimate of SEA ( $\text{SEA}_B$ ) to make comparisons of the sizes of the ellipses. Both  $\text{SEA}_C$  and  $\text{SEA}_B$  are not affected by the sample size, providing a good and more comparable description of the isotopic niche for the different groups analyzed (Jackson *et al.* 2011); in this case between resident and transient bottlenose dolphins. Additionally, we calculated the proportional trophic niche width overlap between resident and transient dolphins (as percentage of the smaller ellipse) to specify similarities of niche extents and niche position (Hahn *et al.* 2013). The niche metrics,  $\text{SEA}_C$ ,  $\text{SEA}_B$  and niche overlap were calculated using the SIBER package of SIAR in R (Parnell *et al.* 2008).

Data were tested for normality and homogeneity of variances using Shapiro-Wilk and Levene tests, respectively. We used a Welch *t*-test, which assumes unequal variance, to test for differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopes between resident and transient dolphins. Significance level was set at 95% for all statistical tests. Results are reported as mean  $\pm$  standard deviation (SD) unless otherwise stated. All statistics were performed using R (R Development Core Team 2011).

The mean values of  $\delta^{13}\text{C}$  for the resident and transient bottlenose dolphins were  $-16.0\text{‰} \pm 0.2\text{‰}$  and  $-16.0\text{‰} \pm 0.3\text{‰}$ , respectively. The mean values of  $\delta^{15}\text{N}$  were  $20.1\text{‰} \pm 0.3\text{‰}$  and  $20.1\text{‰} \pm 0.6\text{‰}$  for the resident and transient group, respectively (Table 1). No differences were found between groups, either for  $\delta^{13}\text{C}$  ( $t_{38} = 0.46$ ,  $P = 0.65$ ) or  $\delta^{15}\text{N}$  values ( $t_{38} = -0.25$ ,  $P = 0.81$ ).

The relative sizes of CR, NR, and TA between resident and transient bottlenose dolphins indicate that the niche width was broader in transient individuals (Table 1). A higher value of  $\text{SEA}_C$  was obtained in the transient group, although it was not

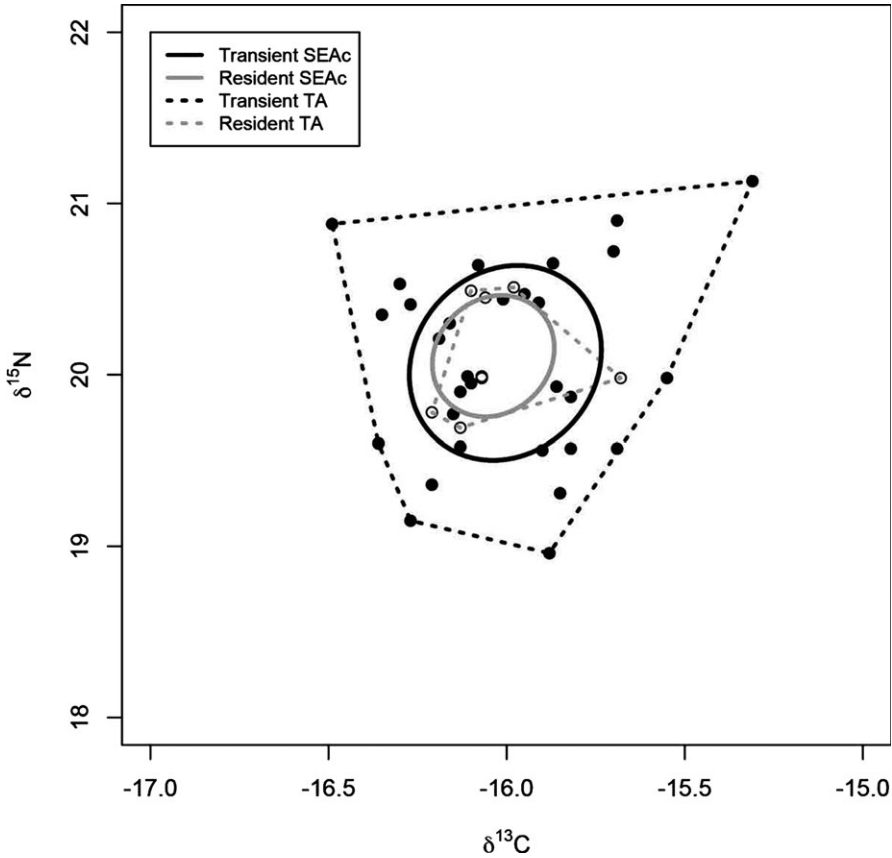


Figure 2.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  biplot for resident (open circles) and transient (closed circles) bottlenose dolphins. Standard ellipses corrected for small sample sizes ( $\text{SEAc}$ ) represent the core niche area of each group (Jackson *et al.* 2011). Convex hulls represent the overall niche diversity and encompass all data points (Layman *et al.* 2007).

significantly different from values in the resident group ( $P = 0.19$ ). The overlap in the isotopic niches of the groups was 100% (Fig. 2).

To our knowledge, this is the first study that analyzes the trophic interactions of bottlenose dolphins in Chile using stable isotope analyses. Although behavioral differences have been previously described between resident and transient individuals in the study area (Thomas 2005, Santos 2013), similar  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotope values in conjunction with an overall isotopic niche overlap suggest similar feeding ecology between resident and transient dolphins that live in sympatry in the north-central coast of Chile.

Similar isotopic niche width metrics in addition with a complete isotopic niche overlap between resident and transient bottlenose dolphins could indicate no trophic niche segregation, suggesting that they forage in similar habitats and occupy equivalent trophic positions. Similar results were reported in two sympatric groups of Indo-Pacific bottlenose dolphins by Kiszka *et al.* (2012), who suggested that two

communities with different ranging and habitat use patterns most likely use similar resources. On the contrary, Fernández *et al.* (2011) reported isotopic differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in two sympatric populations of bottlenose dolphins, suggesting the existence of habitat segregation (coastal *vs.* pelagic) and resource partitioning to reduce potential intraspecific competition. It is important to note that similar isotopic values do not necessarily indicate the same feeding strategy or an overlap in the diet composition, because similar  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotope values may be produced by a diet composed of different prey species with similar isotopic signatures (Browning *et al.* 2014). Thus to elucidate the feeding ecology of the resident and transient bottlenose dolphins in the study area, we recommend that future studies combine the use of isotopes with other dietary complementary methods, such as the collection of fecal samples, stomach content analysis of stranded animals, fatty acids and/or behavioral observations (Kiszka *et al.* 2012).

According to niche theory, a similar trophic niche in two populations or species suggests that the availability of food resources is not a limiting factor (Pianka 1974). Also, it is predicted that species with similar niches would prey upon the same species when a particular prey species is abundant and widespread (Krebs *et al.* 1977). As mentioned above, the study area is a highly productive system (Thiel *et al.* 2007), thus, this scenario may allow both resident and transient bottlenose dolphins coexisting without the need for using different resources, as has been indicated for other sympatric species of cetaceans (*e.g.*, harbor porpoises, *Phocoena phocoena*, and Dall's porpoises, *Phocoenoides dalli*; Nichol *et al.* 2013).

Additionally, we found that the isotopic niche width was greater in the transient dolphins. Although the value of  $\text{SEA}_C$  was not significantly different between the two groups, our results suggest that transient bottlenose dolphins probably use a wider range of prey than resident individuals. This was also apparent in the ranges of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , which showed higher variation among transient individuals (particular NR). Nevertheless, these results should be taken with caution because some community-wide metrics in resident dolphins could be biased due to low sample size (Sv aranta *et al.* 2013).

This study provides valuable ecological information for bottlenose dolphins in a spatial fine scale, becoming the first approximation to the understanding of the trophic ecology of this species in the Humboldt Current System. Future studies on these populations should address a more specific characterization of each population, considering more comprehensive research including genetic and behavioral differentiation factors together with more extensive and comparative dietary research. All this information may actively contribute to the administration plan and conservation strategies design for bottlenose dolphins in these marine protected areas in Chile.

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