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> Insight into niche separation of Risso's dolphin (*Grampus* griseus) in the southwestern South Atlantic via δ^{13} C and δ^{15} N values

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Risso's dolphin, *Grampus griseus*, is a small cetacean distributed worldwide in temperate and tropical oceans (Baird 2009). The distribution of this species in Argentine waters is not clear but appears to be continuous (Bastida *et al.* 2007), and includes the northern coast of Tierra del Fuego. Twelve mass strandings and 13 single strandings have been reported for Tierra del Fuego (Goodall *et al.* 2008), however, mass strandings are generally considered uncommon for this species (Baird 2009).

Grampus typically inhabit oceanic waters associated with slope break boundaries (water depths of \sim 400–1,000 m), but normally dive to depths of <50 m with maximum dives times of 10–30 min (Baumgartner 1997, Olavarría *et al.* 2001, Cañadas *et al.* 2002, Wells *et al.* 2009). Grampus are believed to forage on neritic and mesopelagic oceanic squids that make vertical movements to surface waters at night. Sighting records suggest that Grampus usually live in subgroups of \sim 10–30 animals (Baird 2009, Pereira 2008). Observations of captive animals and mass

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strandings indicate that cohesive subgroups may be composed of same sex and similar aged individuals (Baird 2009, Bearzi *et al.* 2010), and therefore sex- and age-related dietary preferences may result from this behavior (Cockcroft *et al.* 1993). Also, large aggregations of *Grampus* can occur in response to abundant but ephemeral pulses of productivity related to oceanographic fronts that attract their primary prey squid (Davis *et al.* 2002, Bearzi *et al.* 2010). As in other regions, *Grampus* have also been observed in inshore waters at specific times of the year in several areas of the southwestern South Atlantic, including central Patagonia (Reyes 2006) and Península Valdés (Würsig and Würsig 1980; R. Bastida, personal observation). Sighting records suggest that this species may move seasonally between inshore and offshore waters (Best 2007).

The ecology of *Grampus* in the southwestern South Atlantic has never been intensively studied. Little is known about its food habits, distribution, movements, seasonal occurrence, reproduction, or population structure, likely because it inhabits offshore waters and there are few sighting and stranding records along the remote coasts in this region. Nevertheless, bone collected during several stranding events in Tierra del Fuego provides a unique opportunity to study the ecology of this species via stable isotope analysis (SIA).

Recently, SIA of bone collagen from 48 *Grampus* individuals that stranded in NE Tierra del Fuego showed a striking bimodal distribution in both mean δ^{13} C and δ^{15} N values (Riccialdelli *et al.* 2010). These specimens were treated as two feeding groups, GG1 (n = 23 individuals) and GG2 (n = 25 individuals) and we speculated that they inhabited different feeding grounds at different latitudes in the southwestern South Atlantic Ocean.

Since SIA offers information on both dietary and habitat preferences (Syväranta and Jones 2007, Newsome *et al.* 2009) it would be a useful tool to evaluate aspects of the ecological niche of *Grampus* that are difficult to characterize using traditional approaches (*e.g.*, observation or stomach content analysis). δ^{15} N differences between top consumers and particulate organic matter or primary consumers provide a way of estimating the trophic level of *Grampus* (*e.g.*, Cabana and Rasmussen 1996, Post 2002). δ^{13} C values can be used to characterize habitat preferences since carbon isotope values differ between inshore and offshore marine food webs (DeNiro and Epstein 1978, Clementz and Koch 2001)

Differences in baseline (*i.e.*, base of the food web) δ^{13} C and δ^{15} N values have been reported in particulate organic mater (POM) and plankton along latitudinal and longitudinal gradients in different parts of the world, including the southern waters of Argentina (Rau *et al.* 1982, Dunton *et al.* 1989, Goericke and Fry 1994, Schell *et al.* 1998, Lara *et al.* 2010). These baseline differences cascade up food webs to top marine consumers allowing for the study of movement patterns, migration and even stock distinction in marine mammals (*e.g.*, Best and Schell 1996, Walker and Macko 1999, Witteveen *et al.* 2009). Comparison of *Grampus* δ^{13} C and δ^{15} N values with that of baseline POM (or plankton) values if available, or with putative prey collected in different regions/habitats, is the most direct approach to assess its habitat use and movement patterns (*e.g.*, Burton and Koch 1999, Das *et al.* 2003, Witteveen *et al.* 2009). In this study, we attempt to determine what is driving the observed isotopic differences among *Grampus* stranded in Tierra del Fuego through examination of their isotopic variance, estimated trophic level, and comparison with the isotopic composition of putative prey collected in northern and southern waters off Patagonia. We also investigate the effects of maturity class and sex on isotopic composition since age- and sex-related trophic preferences that have been observed in other populations of *Grampus* (Cockcroft *et al.* 1993) could be expressed as isotopic differences (Niño-Torres *et al.* 2006, Knoff *et al.* 2008, Drago *et al.* 2009).

The specimens analyzed are curated in the Goodall collection at the Museo Acatushún de Aves y Mamíferos Marinos Australes in Estancia Harberton Tierra del Fuego, Argentina. Bone fragments were sampled from crania and chevron bones of 48 individuals, including 24 males, 5 females, and 19 individuals of unknown sex. When possible, sex was determined by external examination, which could be confirmed with most specimens *via* direct observation while the carcass was still fresh (n = 21), or by the pelvic bones collected (n = 8); pelvic bones of males are much larger than females (Goodall, personal observation). However, sex identifications have not yet been confirmed by DNA analysis, so the sexual comparisons made here should be considered preliminary (Table S1).

Geographical variation in the body size of *Grampus* populations has been reported previously. Grampus individuals can live up to \sim 35 yr (Baird 2009) but reach sexual maturity between 8 and 10 yr, which corresponds to between \sim 240 and 300 cm in total body length (TBL) (Kruse et al. 1999, Amano and Miyazaki 2004, Chen et al. 2010). Currently, there are no published descriptions of Grampus individuals from South American waters. The largest animal in our study measured 338 cm and 21 animals measured >300 cm in TBL. Therefore, the majority of our animals were likely sexually mature. Because we lacked data on age for most of the specimens, sexual maturity was approximated by TBL as estimated by Amano and Miyazaki (2004) for Grampus populations in waters off Japan. Specimens of both sexes >270 cm in total body length were considered sexually mature (M), and those <270 cm were considered to be sexually immature (I) (Table S1). Since we could only estimate sexual maturity, we also assessed the state of epiphyseal fusion to the vertebra as a level of physical maturity: where 0 = fetus or neonate, with at least some neural spines unfused to the centra; 1 = juvenile, all neural spines fused but epiphyses unfused to the centra; 2 = subadult, some or nearly all of the epiphyses fused; and 3 =adult, all epiphyses fused (Table S1) (Goodall *et al.* 1988, 2008).

A total of ~69 individuals of *Grampus griseus* stranded in Tierra del Fuego, but only 48 individuals were sampled for isotopic analysis. Most were associated with 10 mass stranding events that occurred from 1980 to 1999 and consisted of between 2 and 15 individuals (Goodall *et al.* 2008). Most mass stranding events involved 3–4 individuals except for two instances at Bahía San Sebastián ($53^{\circ}10$ 'S, $68^{\circ}30$ 'W) in northern Tierra del Fuego, Argentina, where 15 individuals stranded during each event (Fig. 1). The first large stranding was found in December 1990 and the second in November 1992, but both groups stranded several months earlier. All of these cases occurred in or within close proximity to Bahia San Sebastian (Fig. 1).



Figure 1. Location of strandings of Risso's dolphin (*Grampus griseus*) in Tierra del Fuego, Argentina. Single strandings: squares. Mass strandings: closed circles denote large events of 15 individuals, open circles denote small events of two to seven individuals.

Bone samples were treated according to Riccialdelli *et al.* (2010), and isotopic results are expressed in delta (δ) notation as explained there. The within-run standard deviation (SD) of an acetanilide standard was $\leq 0.2\%$ for both δ^{13} C and δ^{15} N values. The weight-percent [C]/[N] ratios of all specimens were in the expected range (2.8–3.5) for pure protein (Ambrose 1990).

In order to calculate trophic level (TL) in a comparable fashion as previous studies in the region, we used the isotopic baseline of Forero *et al.* (2004) and Ciancio *et al.* (2008). As assumed in Riccialdelli *et al.* (2010), GG1 was associated with central-northern food webs and GG2 with southern food webs off Patagonia. In this manner, we estimated the TL of GG1 using the mean δ^{15} N value (16.4‰ ± 0.1‰) and TL (3.2) of Argentine anchovy (*Engraulis anchoita*) utilized by Forero *et al.* (2004) as a baseline for the northern Patagonia food web. For GG2, we used the TL estimated in Riccialdelli *et al.* (2010) that utilized the mean δ^{15} N value (7.3‰ ± 0.8‰) and TL (2.0) of euphausids in Ciancio *et al.* (2008). Since differences in prey choice among individuals from the same group (GG1 or GG2) could affect the variation in the relative trophic position of that group, we calculated TL separately for each individual and reported a mean and variance in trophic level for each *Grampus* group. The TL of each individual of *Grampus* was then calculated according to Riccialdelli *et al.* (2010).

In order to test for differences in estimated TLs between groups and to test for differences in isotope values between sex and maturity classes in each group, a Kolmogorov-Smirnov test (*K*-*S*-test) was employed to test for normality in δ^{13} C and δ^{15} N. We used an *F*-test to test homogeneity of variance. Pairwise comparisons were performed using a Student's *t*-test when data met parametric requirements; otherwise a nonparametric Kruskall-Wallis *H*-test and Mann Whitney *U*-test were employed for the two variables (δ^{13} C and δ^{15} N) to test for differences in isotope values between categories (TLs, sex, and maturity classes) of each group. We assessed variance in δ^{13} C and δ^{15} N using an *F*-test as a method to assess overlap/segregation between individuals of different sexes and maturity classes in each group (GG1 or GG2). Lastly, a Spearman rank correlation (ρ , Spearman *rho* coefficient) was performed to evaluate a possible relation between the isotopic variability found in *Grampus* individuals and the stranding year. For this we assumed the existence of a single group that includes all the specimens analyzed. For all calculations, we tested significance at the $\alpha = 0.05$ level.

In 6 of the 10 mass stranding events all individuals analyzed are similar to one group or the other (GG1 or GG2). In the other four mass stranding events, there was a mixture of individuals that appeared to be related to both GG1 and GG2 groups. A first case involved two individuals that stranded together but had distinct isotope values corresponding to the two groups. A second case, involved three animals, but we were only able to analyze two of them and each had distinct isotope values that corresponded to either the GG1 or GG2 groups. In the third case, we only analyzed three individuals that stranded in a group of seven; one of these animals had isotope values similar to the GG1 group and the other two were similar to GG2. The last case involved two individuals in the first large mass stranding event that occurred in 1990 (n = 15) that had isotope values similar to GG1 group; the other 13 animals in this event correspond to GG2. The second large mass stranding (n = 15) that occurred in 1992 contained only animals associated with the GG2 group. Despite the longterm bonds between adult males and between adult females, subadult individuals of *Grampus* have less stable associations than those observed for adults (Hartman et al. 2008), and at an age likely corresponding to reproductive maturity they leave their natal groups to join others or to form new pods. In these cases, if the tissue analyzed represented ecological information prior to the movement from one group to another, their isotopic signatures may reflect the original signature of the previous group if the environment in which they now live/feed is isotopically distinct from their natal region (Hobson 2007). This may have occurred in some stranding events in which we found a mixture of individuals that corresponded to both the GG1 and GG2 groups.

Since the TL calculated for the individuals in each group was normally distributed (*K-S*-test, P > 0.15) and each group had similar variance (*F*-test = 0.764, P = 0.529), we used a *t*-test to compare TL estimates between GG1 and GG2. GG2 had a significantly higher mean TL (\pm SD) of 4.4 (\pm 0.4) than GG1 (4.1 \pm 0.4), (*t*-test = 2.8393, P = 0.0067).

A comparison of isotope values for the different sexes in both groups (GG1 and GG2) showed no significant differences between females and males in δ^{13} C (*U*-test, P = 0.6356 for GG1 and P = 0.8137 for GG2) or δ^{15} N values (*U*-test, P = 0.5147 for GG1 and P = 0.9062 for GG2). There were no significant differences in isotopic

variance for δ^{15} N between females and males in either group (F = 0.338, P = 0.0848 for GG1; F = 0.5894, P = 0.229 for GG2) or in δ^{13} C (F = 0.7046, P = 0.5744) for GG2. For GG1, variation in δ^{13} C among females was slightly higher than for males (F = 0.0464, P = 0.045).

According to our estimates of physical maturity only one animal was a juvenile; 42 were subadults, three were adults, and two were unknown. We found no statistical differences among physical maturity classes for either group in mean δ^{13} C (*H*-test, P = 0.728 for GG1 and *U*-test, P = 0.3405 for GG2) or δ^{15} N values (*H*-test, P = 0.552 for GG1 and *U*-test, P = 0.2924 for GG2). Sub-adult individuals had a higher degree of variation in δ^{13} C than adults in GG2 (Leven's test = 4.371, P = 0.048). We could not compare the isotopic variation in GG1 due to the low number of samples in the juvenile and adult categories. In regards to sexual maturity, we found no statistical differences between sexually immature and mature individuals in either group (GG1 or GG2) of *Grampus* in δ^{13} C (*U*-test, P = 0.4240 for GG1 and P = 0.1381 for GG2) or δ^{15} N values (*U*-test, P = 0.6478 for GG1 and P = 0.2317 for GG2).

Despite evidence of resource partitioning between sexes and age classes of *Grampus* found in South African waters (Cockcroft *et al.* 1993), we found similar mean isotope values among sexual and physical maturity classes in the GG1 and GG2 groups, suggesting similar foraging behavior. Unfortunately, most individuals in the GG1 and GG2 groups were sexually mature males, thus future analysis that includes a more even sex ratio and distribution of age classes will be required to better examine sex- and age-related food and habitat preferences.

We found a significant negative correlation in δ^{13} C and δ^{15} N values of *Grampus* through time (1980–1999; $\rho = -0.5009$, P < 0.001 for δ^{13} C; and $\rho = -0.5707$, P < 0.001 for δ^{15} N; Table S1). The significant decrease in both isotope values in *Grampus* bone collagen collected from Tierra del Fuego animals over a span of ~20 yr could be the result of several scenarios: (1) a change in baseline isotope values of the entire food web over time; (2) a change in foraging habitats from inshore to offshore areas, which may correspond to a change in prey preferences; (3) a north to south latitudinal shift in foraging grounds at the continental shelf/slope boundary, which may also be associated with a change in prey preferences; (4) a shift in consumption of high to low trophic level prey; or (5) the existence of two groups that forage in areas with different baseline isotope values. The relatively short period of time over which most individuals stranded (n = 35 from 1990 to 1992), the advanced maturity estimated for most individuals, and the type of tissue analyzed (bone collagen) are all critical elements for evaluating the relative role of these possible explanations.

For a mammal the size of an adult *Grampus*, the isotopic composition of bone collagen likely integrates several years of ecological information. While the isotopic composition of bone and tooth dentine collagen from marine top consumers has been used to assess long-term (multiannual to decadal) shifts in foraging ecology and food webs (Hirons *et al.* 2001, Newsome *et al.* 2007), bone collagen does not track short-term (*i.e.*, seasonal or annual) dietary shifts or changes in baseline isotope values that results from variation in productivity, nutrient availability, or temperature. Since most individuals (n = 35) we analyzed stranded over a short time period from 1990

to 1992, the large degree of variation in both δ^{13} C (range = -15.6% to -10.9%) and δ^{15} N (range = 13.1‰-21.6‰) values was not likely driven by systematic short-term (seasonal or annual) changes in (1) baseline isotope values, (2) foraging habitat from inshore to offshore, (3) foraging habitat from northern to southern waters, or (4) the consumption of high *vs.* low trophic level prey.

The conditions described above, however, do not constrain two other possible explanations for the significant decrease in *Grampus* δ^{13} C and δ^{15} N values through time. This trend could result from two groups that (1) feed in the same region but feed on prey that is isotopically distinct for reasons related to taxonomy or size, or (2) feed on similar prey that occur in different regions (*e.g.*, north *vs.* south) of the southwestern South Atlantic that have distinct baseline isotope values.

To further constrain these possible explanations, we compared *Grampus* isotopic data with that of potential prey collected from northern and southern areas of the southwestern South Atlantic. While we lack any dietary data derived from stomach contents for *Grampus* in Tierra del Fuego, other populations are known to feed almost exclusively on squid (Baird 2009). Our squid isotopic data is restricted to a few commercially exploited species (e.g., Illex argentinus, Loligo gabi, L. sanpaulensis), which are also the most abundant squid inhabiting the neritic waters off Patagonia (Dawe and Brodziak 1998). In this region, squid have low $\delta^{15}N$ values relative to fish (Riccialdelli *et al.* 2010), although body size and δ^{15} N values are positively correlated for several squid species (Cherel and Hobson 2005). After application of 5.0% and 3.4% to measured δ^{13} C and δ^{15} N signatures to account for trophic and tissue discrimination (Hedges et al. 2005, Caut et al. 2009), mean GG2 values are very similar to those of squid reported by Ciancio et al. (2008) and Riccialdelli et al. (2010) for southern Patagonian waters (Table 1, Fig. 2). Likewise, trophic-corrected mean isotope values for GG1 are similar to isotope values of squid for central and northern Patagonian waters reported by Forero et al. (2004), Lewis et al. (2006), and Drago et al. (2009) (Table 1, Fig. 2).

Prey types found at a higher trophic level and thus have higher δ^{15} N values than pelagic squids, such as benthopelagic fishes that occur in continental shelf habitats (e.g., Merluccius hubbsi, M. australis, and Salilota australis; Riccialdelli et al. 2010), are believed to be a supplementary dietary item for Grampus (Sekiguchi et al. 1992, Best 2007). The slightly but significantly higher TL estimated for the GG2 group (4.4 ± 0.4) in comparison to GG1 (4.1 ± 0.4) suggests that Grampus from southern Patagonian waters may supplement their diet with benthopelagic fishes. Despite this small but significant difference in estimated trophic level, both groups were feeding at roughly the same trophic level (TL: 4.0-4.5), which is similar to the global estimate of 4.3 for Grampus derived by standardized diet composition based on stomach contents (Pauly et al. 1998).

Overall, our study shows that isotopic analysis is useful for differentiating between spatially segregated groups of the same species that may correspond to different genetic stocks. Future genetic (mtDNA and nuclear DNA) and additional isotopic analyses of South American *Grampus* specimens may possibly confirm the presence of two distinct stocks that correspond to the isotopically distinct groups described here. These complimentary approaches will aid conservation and management of this species in the southwestern South Atlantic Ocean by providing geographical

<i>laur</i> 1. O C and O N values and standard deviations (c Patagonian waters, South Atlantic Ocean. na = not available.	Dean. na = not availous (2) Dean. na = not available.		e sampres	to possibi	e prey spe		поглиет	vatues and standard deviations (SD) for muscle samples of possible prey species from normern and soumern faituates of fantic Ocean. na = not available.
		δ ¹³ C		$\delta^{15}N$	Z	C/N		
Species (common name)	Sampling location	Mean	SD	Mean	SD	ratio	и	Reference
South Patagonian waters								
<i>Loligo gabi</i> (Patagonian squid)	53°09'S, 62°48'W	-17.5	0.3	13.3 12.6	0.5	3.2	10	Riccialdelli et al. (2010)
Semirrosia tenera (lesser bobtail	\sim 52°S, 65°W ^a		0.0 na	12.3	u./ na	na na	1	Ciancio et al. (2008) Ciancio et al. (2008)
squa <i>)</i> <i>Ilex</i> spp. (Argentine shortfin souid)	53°09′S, 62°48′W	-16.6	na	14.9	na	3.3	1	Riccialdelli et al. (2010)
Illex argentinus (Argentine	\sim 53°S, 65°W ^a	-18.1	0.3	13.1	0.9	na	12	Ciancio et al. (2008)
Morotentus squacy Morotenthis ingens (greater hooked squid)	\sim 52°S, 65°W ^a	-18.7	0.4	13.5	1.1	na	7	Ciancio <i>et al.</i> (2008)
North Patagonian waters Loligo sanpaulensis (South	42°59'S, 62°27'W	-16.8	0.2	17.2	0.3	na	\sim	Drago <i>et al.</i> (2009)
American iongun squid) Loligo gabi (Patagonian squid)	42°59′S, 62°27′W	-17.6	0.4	15.7	0.6	na	4	Drago et al. (2009)
Loligo + Illex spp.	~ 42 'S, $63^{\circ} - 60^{\circ}$ W ^a	-17.0	0.5	16.3	0.5	na	17	Forero et al. (2004)
Illex argentinus (Argentine	47°10′S, 64°39′W	-17.0	0.6	13.7	0.8	na	2	Drago et al. (2009)
suorum squad)	51°27′S, 65°45′W 51°27′S, 65°45′W	-17.6 -17.4	$0.2 \\ 0.1$	$14.9 \\ 16.2$	0.5 0.2	na na	1 7	Lewis <i>et al.</i> (2006) Lewis <i>et al.</i> (2006)
^a Sampling location from Forero <i>et al.</i> (2004) and Ciancio <i>et al.</i> (2008) are approximated according with sampling details explained in these papers	I. (2004) and Ciancio et al.	. (2008) are a	pproxima	ited accord	ng with s	ampling d	etails exp	plained in these papers.

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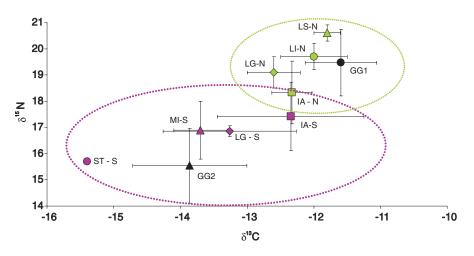


Figure 2. Bone collagen mean δ^{13} C and δ^{15} N values (\pm SD) of Risso's dolphin (*Grampus griseus*) groups and possible prey species from subantarctic waters of the South Atlantic Ocean. GG1 (\bullet) north ecotype. GG2 (\blacktriangle) south ecotype. Prey values have been corrected for trophic discrimination by adding 5.0% and 3.4% to δ^{13} C and δ^{15} N values respectively. Northern prey: *Loligo sanpaulensis* (LS-N. \blacktriangle). *Loligo gabi* (LG-N. \diamond). *Illex argentinus* (IA-N. \blacksquare). *Loligo* and *Illex* spp (LI-N. \bullet). Southern prey: *Loligo gabi* (LG-S. \diamond). *Illex argentinus* (IA-S. \blacksquare). *Moroteuthis ingens* (MI-S. \blacktriangle). *Semirrosia tenera* (ST-S. \bullet). Circles represent predator-prey associations in the northern (green dotted line) and southern (purple dotted line) regions.

and genetic structure to the population, which is currently lacking for *Grampus* in this region.

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SUPPORTING INFORMATION

The following supporting information is available for this article online:

Table S1. Southwestern South Atlantic Risso's dolphins (*Grampus griseus*) bone collagen isotope composition. δ^{13} C and δ^{15} N values and C/N ratios of each *Grampus* individual analyzed. Location of stranding: Bahía San Sebastián (BSS; 53°10'S, 68°30'W), Estancia Cullen (Cullen, 52°52'S, 68°27'W), Los Chorrillos (52°21'S, 68°13'W), Punta María (53°57'S, 67°27'W). Maturity classes were determined using two methods. First, by epiphyseal fusion: 1 = no fusion; 2 = subadult, partly fused; 3 = adult, all epiphyses fused. Second, by total body length (TBL):

M = sexually mature individuals (>270 cm total length), I = sexually immature individuals (<270 cm total length). ND = not determined. Determination of sex: M, F = from intact animal; (M), (F) = from pelvic bones, ND = not determined. All specimens (RNP Goodall collection) are archived in the Museo Acatushún de Aves y Mamíferos Marinos Australes, Estancia Harberton, Tierra del Fuego, Argentina. We separated the individuals into two groups (GG1 and GG2) as suggested by Riccialdelli *et al.* (2010).