Spatial genetic structure of dusky dolphin, Lagenorhynchus obscurus, *along the argentine coast: preserve what scale?*

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ABSTRACT

1. The dusky dolphin (*Lagenorhynchus obscurus*) represents one of the most abundant species of small cetacean in Argentine waters. During the 1980s and 1990s, high levels of incidental mortality in purse and trawl fisheries were documented, and in recent decades tourism activities have been added as a potential source of disturbance.

2. The study objectives were to identify spatial genetic structure and regional genetic patterns of dusky dolphins along the Argentine coast. The variation of 413bp of the control region of 119 individuals over six locations spread along 2800 km (38°40'S to 54°30'S) was examined. Spatial genetic analyses, SAMOVA, genetic landscape shapes and autocorrelation analyses were conducted.

3. The most probable configuration was K=2, island population vs. continental populations ($F_{CT} = 0.774$) and the spatial autocorrelation analysis showed a strong regional genetic structure, defining an operational unit at < 50 km.

4. The results provide valuable information that should be taken into account in the development of conservation strategies and management of the species; making the efforts focus on conserving vulnerable dusky dolphin groups by protecting their preferred coastal shallow habitat and by monitoring and regulating the dolphin watching and fishing activities, acting upon local populations along the Argentine coast. Copyright © 2015 John Wiley & Sons, Ltd.

INTRODUCTION

Assessing population structure among continuously distributed animals is one of the most challenging and vital aspects for managers and conservationists (Amos and Balmford, 2001;

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Hey and Machado, 2003). In the marine environment, this problem is further complicated by the fact that many species are continuously and homogeneously spread over large areas, thus understanding population structure is a key component of management efforts (Waples, 1998; King and Burke, 1999; Palumbi, 2003). In some cases where species' population structure is already known, specific protected areas can be created to help conserve as much of the genetic

diversity of the species as possible. Cetaceans provide good examples of this kind of species. Despite their broad range and their dispersal capabilities, many cetaceans often show strong genetic structure at local or even fine scale (Hoelzel, 1998b). It is usually argued that these patterns, not always correlated with geographic features, are more likely related to a combination of behaviours, such as specializations for local resources, or social organization (Hoelzel, 1998b; Hoelzel *et al.*, 2002). Natoli *et al.* (2005) suggested that bottlenose dolphins show a relationship between habitat type and group strategies for resource exploitation in regional populations, promoting philopatry and population genetic isolation. Addressing such questions about the structure of complex populations requires the integration of landscape ecology, spatial statistics and population genetics (Manel *et al.*, 2003; Stofer *et al.*, 2007). In contrast to traditional population genetics studies, such as tests of isolation-by-distance, landscape genetics provides a framework for testing the relative influence of landscape features on genetic diversity, gene flow, genetic discontinuities (Guillot *et al.*, 2005) and genetic population structure (Manel *et al.*, 2003; Holderegger and Wagner, 2006). Additionally, spatial genetic analyses can provide knowledge about dispersal capabilities, population demography and reproductive strategies (Miller *et al.*, 2006; Lowther *et al.*, 2012; Vera Escalona *et al.*, 2012). Despite advances in molecular techniques for assessing genetic variability, the main problem is defining practical criteria for establishing evolutionarily significant units (ESUs) and managements units (MUs) for conservation (Moritz, 1994a, b; Newton *et al.*, 1999; Crandall *et al.*, 2000). Both criteria have been criticized. Alternatively, Diniz-Filho and Telles Pires de Campos (2002) proposed to evaluate and explore the genetic variability in geographic space, establishing the optimum strategies to deal with and preserve the actual genetic variability through the definition of geographic extent of operational units to be used in conservation. The authors applied this new concept to a variety of species, from plants to bears, illustrating the utility of this new approach (Diniz-Filho and Telles Pires de

Campos, 2002). From a conservation perspective, these analyses can be invaluable for defining conservation units for species management purposes (Moritz, 1994a, b) and to establish operational units for intraspecific conservation and management, particularly when dealing with continuously distributed populations (Diniz-Filho and Telles Pires de Campos, 2002). Marine mammals are currently facing conservation problems related to the habitat on which they depend for survival while some of the greatest threats are in extractive activities such as fishing (unsustainable use, incidental mortality, etc.) (Reeves *et al.*, 2003).

The Argentine Sea has been exploited in the past three decades by fishing activities, exploration and transportation of oil, bilge cleaning and cetacean-based tourism. This ecosystem includes many different top predators, among which is the dusky dolphin, *Lagenorhynchus obscurus*, listed as 'Data Deficient' by the International Union for the Conservation of Nature (IUCN Red List) (Hammond *et al.*, 2008). The species is subject to multiple anthropogenic impacts along its distribution off the Argentine coast. The dusky dolphins are caught incidentally along the continental shelf, especially where the species interacts with the anchovy fishery in the Buenos Aires province and in the purse seine and trawling fishery at Golfo San Jorge. It has been suggested that bycatch during the 1990s was probably close to the maximum sustainable level (Corcuera *et al.*, 1994; Crespo *et al.*, 1997; Dans *et al.*, 2003). In addition, dusky dolphins are the subject of whale-watching activities at a local scale in Golfo Nuevo, Peninsula Valdes; cetacean-based tourism is one of the fastest growing sectors and provides incomes for people in local communities. Coscarella *et al.* (2003) and Dans *et al.* (2008) evaluated the effect of tour vessels on the behavioural budget of dusky dolphins, and showed that feeding behaviour and energy budgets are affected by the presence of tour boats. Therefore, it is clear that new information is needed to highlight the importance of ecological factors in shaping spatial genetic structure and to define management or operational units to delineate management and conservation strategies for the

species. The objectives of this study were to identify spatial genetic structure and regional genetic patterns of dusky dolphin along the Argentine coast.

METHODS

Sample collection and DNA extraction

Tissue samples were collected along the Argentine coast, from Buenos Aires province (BA), Golfo San Matías (GSM), Golfo San José (GSJ), Golfo Nuevo (GN), Golfo San Jorge (GSJOR) and Ushuaia (U) during 2006–2011 fieldwork seasons seasons (Figure 1). In total, 171 samples were analysed from museums (teeth and bone), stranded animals, biopsy sampling and animals from fisheries bycatch. Biopsy samples were taken as described by Loizaga de Castro *et al.* (2013). Museum samples were mainly from Buenos Aires province (10) and Ushuaia (1); stranded animals, Buenos Aires (1), Golfo San Matías (2), San José (1) and Golfo Nuevo (1); biopsy samples Golfo San Matías (24), San José (26) and Golfo Nuevo (84). The Golfo San Jorge samples (21) were from fisheries bycatch. DNA was extracted from tissue samples preserved in salt saturated 20% DMSO by a standard phenol/chloroform extraction method (Hoelzel, 1998a). DNA was extracted from bone samples using QIAgen polymerase chain reaction (PCR) purification columns after grinding 100 mg of bone and digesting it at 37°C for 48 h in 1 mL of digestion buffer (0.01 mol L^{-1} TRIS, 0.01 mol L^{-1} NaCl, 1% SDS, 2 mg mL^{-1} proteinase K, 0.01 PTB). The extraction and the analysis of the bone specimens were conducted in a different laboratory to avoid contamination.

Mitochondrial DNA analysis

The mitochondrial DNA control region was amplified with the primers MTCRf (5′-TTCCCC
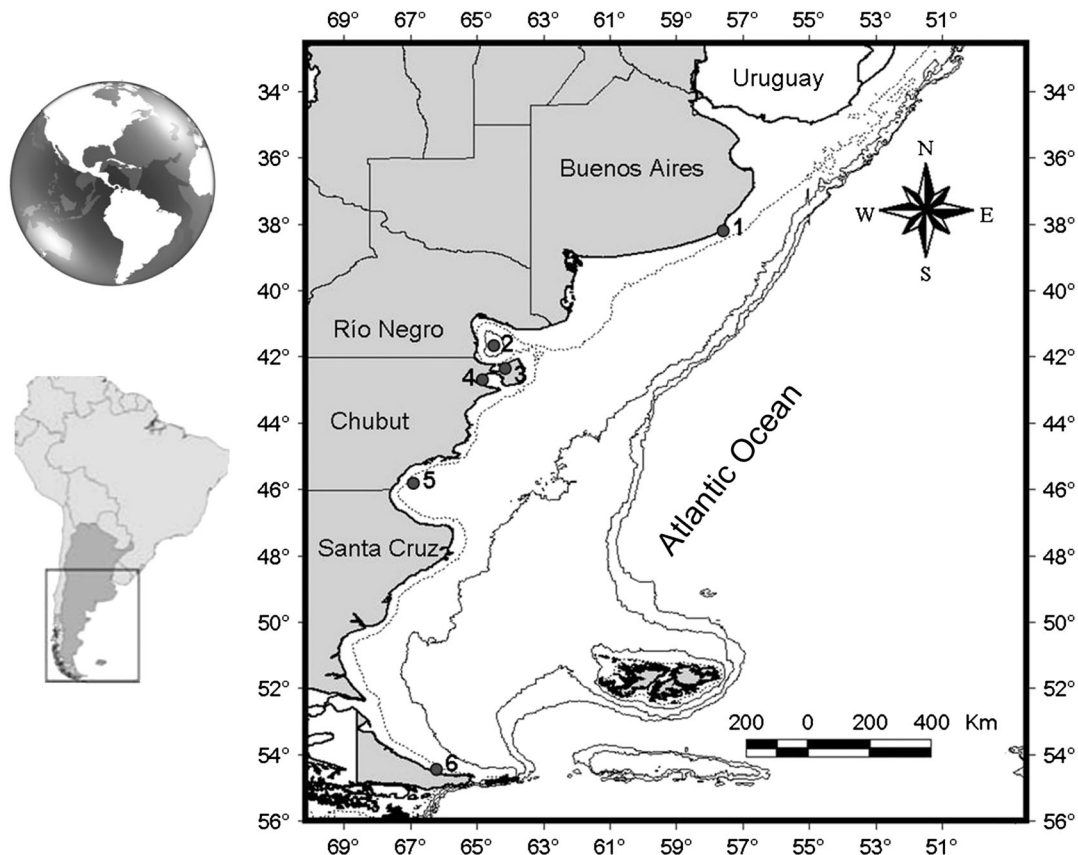

Figure 1. Study area, sampling units consider for *L. obscurus* off Argentine coast: (1) Buenos Aires; (2) Golfo San Matías; (3) Golfo San José; (4) Golfo Nuevo; (5) Golfo San Jorge; and (6) Ushuaia.

GGTGTAAACC) and MTCRr (5′-ATTTTCA GTGTCTTGCTTT) (Hoelzel, 1998a, b) with the following PCR profile: 5 min at 95°C; then 35 cycles of 1 min at 51°C, 1 min 30 s at 72°C and 45 s at 94°C; then 1 min at 51°C and a final extension phase of 8 min at 72°C. All PCRs (25 μL, final volume) contained: 1 μL of DNA template, 10 mmol L^{-1} Tris-HCl (pH 8.4), 2 mmol L^{-1} MgCl$_2$, 200 μmol L^{-1} each dNTPs, 0.3 μmol L^{-1} of each primers and 0.5–1.0 unit Taq polymerase. PCR products were purified with QIAGEN PCR purification columns. Mitochondrial DNA from bone and teeth samples were amplified using two sets of primers Dlp10F (5′- CCACAGTACTATGT CCGTATT) Dlp5R (5′- CATCGWGATGTCTTA TTTAAGRGGAA) (Baker *et al*., 1993). The samples were amplified using the QIAGEN multiplex PCR kit (25 μL, final volume). The PCR reaction conditions were as follows: 1 min at 94°C, then 35 cycles of 1 min at 55°C, 45 s at 72°C and 30 s at 94°C; then a final extension of 5 min at 72°C.

Spatial genetic analyses

Spatial analysis of molecular variance (SAMOVA) (Dupanloup *et al*., 2002) was done to identify partitions of geographically adjacent sampling areas that were maximally differentiated based on sequence data; the analysis defines groups of populations (K) that are geographically homogeneous and maximally differentiated from each other; the method uses the FCT index, which is the proportion of total genetic variance due to differences between groups of populations. Analyses were based on 100 simulated annealing steps and examined maximum indicators of differentiation (F$_{CT}$ values) varying $K = 2$ through $K = 6$ partitions of the sampling areas and each hypothesis tested using AMOVA in Arlequin (Manier and Arnold, 2006). Isolation-by-distance (IBD) was also tested following the procedure implemented in the computer program Alleles In Space (AIS, Miller, 2005). In addition, to identify regional genetic patterns of dusky dolphin along the Argentine coast, spatial autocorrelation analyses were performed using AIS (Miller, 2005). The measure of autocorrelation used for the analysis (*Ay*) was quantified as the average genetic distance between pairs of individuals that fell into distance class *y*. Analyses were initially performed using 10 distance classes and were subsequently repeated using 20, 30, 40 and 50 distance classes to ensure that the arbitrary choice of distance class size had no effect on analysis outcomes. A randomization procedure consisting of 5000 replicates was used to identify distance classes where average genetic distances were significantly larger or smaller than random expectations. Finally, 'genetic landscape shapes', a visualization technique was used to obtain a graphical representation of genetic distance patterns across the landscape using AIS software (Miller, 2005). This procedure was initiated by constructing the Delaunay triangulation-based connectivity network of sampling areas and assigning genetic distances (*Zi*, calculated as the average proportion of nucleotide differences between individuals from different sampling areas) to landscape coordinates at midpoints (*Xi*, *Yi*) of the *n* connectivity network edges. Next, a simple interpolation procedure (inverse distance-weighted interpolation) was applied to infer genetic distances between locations on a uniformly spaced grid overlaid upon the entire sampled landscape. For each grid coordinate (*x*, *y*), a genetic distance, *z*, was inferred from each of the $i = 1$ to *n* genetic distances (*Zi*) assigned to the connectivity network following Miller *et al*. (2006). Following the interpolation procedure, a three-dimensional surface plot was generated to interpolated genetic distances where X and Y coordinates on the plot corresponded to geographical locations on the rectangular grid and surface plot heights (Z) reflected genetic distances. Analyses were performed using a variety of grid sizes (20 × 20, 50 × 50, 100 × 100) and with a range of distance weighting parameters (*a* = 0.5–2) to ensure that interpolation parameters chosen for the analysis did not overly influence interpretations of the graphical depictions generated by the procedure.

RESULTS

The diversity of the dusky dolphin was analysed locally (treating each sampling location as a separate population) and taking all locations as a

Table 1. Distance between sampled localities along the Argentine coast, with latitude and longitude position. Sample size (N), number of haplotypes (n_h), and genetic diversity within the six dusky dolphin populations in terms of haplotype diversity (h), nucleotide diversity (π) and standard deviations, segregating sites (S) are shown

Locality	Distance (km)					Lat-Long	N	N seq	n_h	h	π	S
	BA	SM	SJ	GN	SJOR							
Buenos Aires (BA)						38° 40'S 58° 35'W	11	3	2	0.667 ± 0.314	0.008 ± 0.007	5
Golfo San Matías (SM)	651					41° 32'S 64° 24'W	26	18	12	0.941 ± 0.038	0.011 ± 0.006	18
Golfo San José (SJ)	753	102				42° 20'S 64° 24'W	27	23	11	0.905 ± 0.039	0.008 ± 0.004	13
Golfo Nuevo (GN)	855	382	280			42° 45'S 64° 34'W	85	61	26	0.943 ± 0.014	0.010 ± 0.005	29
Golfo San Jorge (SJOR)	1553	902	800	520		46° 02'S 66° 18' W	21	12	11	0.984 ± 0.04	0.012 ± 0.007	19
Ushuaia (U)	1955	1608	1708	1988	1100	54° 30'S 65° 40'W	1	1	1	1± 0.5		

single population using 413 bp of the mitochondrial control region, which recovered 33 haplotypes from 40 variables sites (GenBank Accession no. KJ207081–KJ207199). The amplified segment was obtained from 119 individuals. The haplotype diversity for the entire population of dusky dolphins was h = 0.85 and nucleotide diversity π = 0.005, showing high levels of genetic variability. The haplotype diversity (h) at the level of local populations showed considerable variation, from h = 0.66 - Buenos Aires to h = 0.98 - Golfo San Jorge. On the other hand, values of nucleotide diversity (π) varied from low (π = 0.0081) to moderate (π = 0.01) (Table 1).

The SAMOVA analyses clearly indicated strong genetic structure along the Argentine coast (Table 2). In analyses where K = 2, partitions of sampling areas were identified that suggested insular vs. continental groups (partitions: BA, SM, GSJ, GN, GSJOR vs. U; FCT = 0.773). In analyses where K = 3, an additional partition was identified in the north of Argentina plus the three northern Patagonian gulfs isolated from southern gulf and insular population (partitions: BA, SM, GSJ, GN vs. GSJOR vs. U; FCT = 0.453). The indicator of differentiation used for this analysis (FCT) was greatest for the K = 2 case, and that FCT values gradually decreased relative to the maximum value in the K = 3–6 analyses. Thus, the analysis suggested the presence of two groups of maximally differentiated sampling areas (partitions: BA, SM, GSJ, GN, GSJOR vs. U; FCT = 0.773). Considering all sampling localities, the correlation coefficient, calculated using the Mantel test between matrices of geographic distance and genetic distance obtained under the model of Jukes and Cantor (1969), was 0.834 P =

Table 2. Spatial analysis of molecular variance, SAMOVA; F_{CT} values obtained from mtDNA control region of dusky dolphins along Argentine coast. (Buenos Aires (BA), Golfo San Matías (GSM), Golfo San José (GSJ), Golfo Nuevo (GN), Golfo San Jorge (GSJOR) and Ushuaia (U))

Groups	K	F_{CT}
BA, GSM, GSJ, GN, GSJOR vs. U	K = 2	0.773
BA, SM, GSJ, GN vs. GSJOR vs. U	K = 3	0.453
BA vs. SM, GSJ, GN vs. GSJOR vs. U	K = 4	0.218
BA, SM vs. GSJ vs. GN vs. GSJOR vs. U	K = 5	0.171

0.007 ($P < 0.01$) (Figure 2) showing an isolation by distance model. Nevertheless, to avoid any bias due to large geographical distances a second analysis, excluding the Ushuaia (insular sampling locality) was conducted and the correlation coefficient was 0.427 $P = 0.197$. Therefore, it was concluded that the population across the continental shelf did not support the isolation by distance model.

Furthermore, autocorrelation analyses performed on the complete data set from the Argentine coast, excluding Ushuaia, clearly indicated the presence of strong regional phylogeographic structure (Figure 2). In analyses performed using 10 distance classes, the data set yielded highly significant values of Ay that were smaller than random expectations over the two shortest distance classes (encompassing geographic distances up to 7 km; $P < 0.01$). Likewise, geographic distances up to 10 and 20 km were smaller than random expectations. Also, the last two distance classes were higher than expected by chance (encompassing geographic distances up to 50 and 100 km). Qualitatively similar results were obtained when z = 20, z = 30, z = 40 and z = 50 distance classes were used for analyses (Figure 2). Thus, the geographic distribution of dusky dolphins shows strong patterns of phylogeographic structuring at a local scale; also dusky dolphins were uniformly distributed and not at random as was expected over 200 km. The operational unit for dusky dolphins can be set at 50 km for management and conservation purposes. This is a minimum linear distance at which dolphin groups are independent.

Overall, the genetic landscape shape interpolation analysis produced surface plots that qualitatively supported results from the SAMOVA analyses (Figure 3). A 'ridge' (indicating greatest
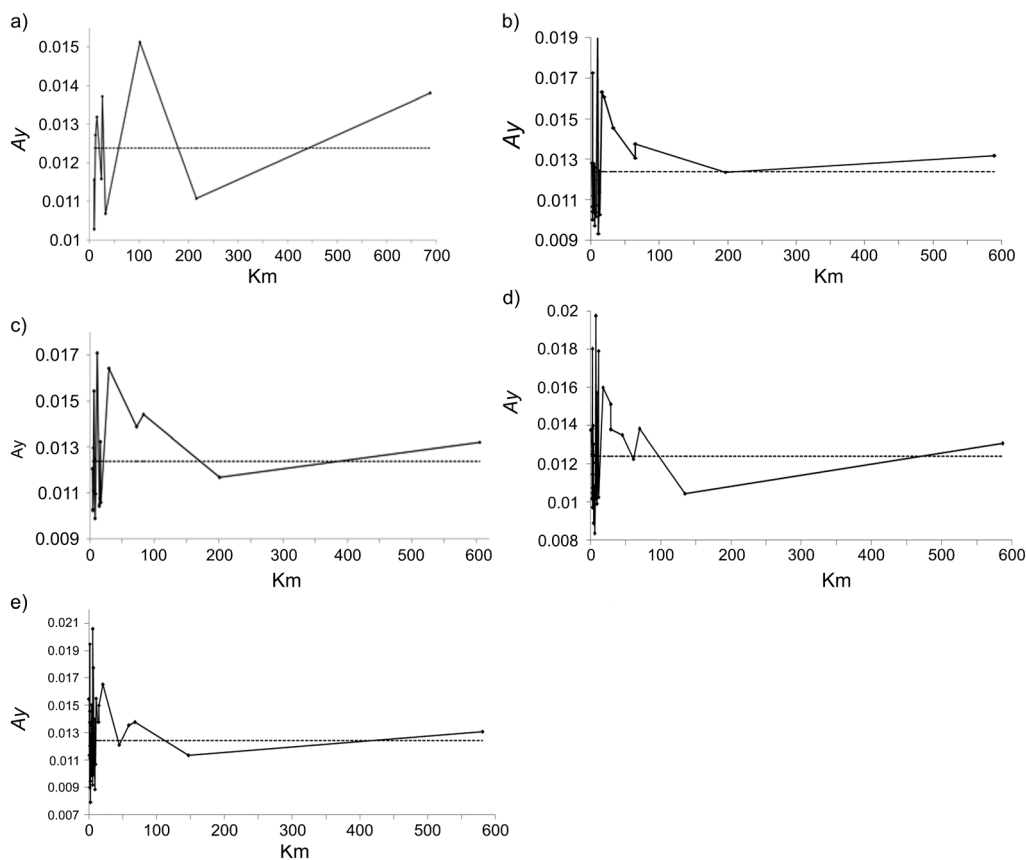

Figure 2. Spatial autocorrelation analyses for dusky dolphin, *L. obscurus*, along the Argentine coast, excluding Usuahia (n=1). Analyses were performed using z = 10, 20, 30, 40 and 50 distinct distance classes. Ay quantifies the average pairwise genetic distances between pairs of individuals that fall within the boundaries specified for distance class y. Horizontal lines indicate the average value of Ay for a data set. (a) z = 10; (b) z = 20; (c) z = 30; (d) z = 40; (e) z = 50 distances classes.
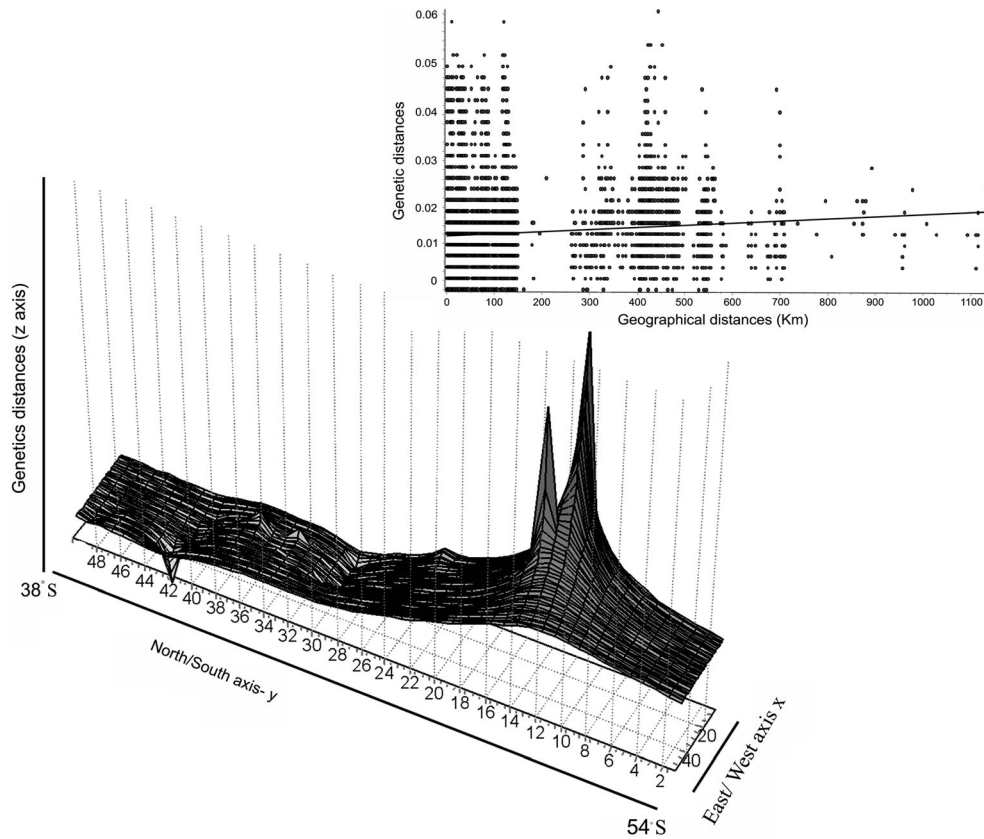
Figure 3. Genetic landscape shape (GLS) interpolation and 'isolation by distance' analysis, for *L. obscurus*. GLS was made by using a 50×50 grid and a raw genetic distance. X and Y axes correspond to geographic locations within the overall physical landscape examined in this study. Surface plot heights reflect genetic distances.

genetic distances) was observed with a north–south orientation, i.e. Ushuaia population, at the southern limit of dusky dolphin distribution, is more genetically distinct from populations along the continental shelf, at the northern and central distribution of dusky dolphin in Argentina. Qualitatively similar depictions were also observed regardless of the rectangular grid size or distance weighting parameter chosen for the analyses (results not shown). Likewise, use of raw genetic distances or residual genetic distances did not have any appreciable effect on analysis outcomes. Specifically, the current analysis indicated that patterns of genetic distances increased with increasing latitude (Figure 3).

DISCUSSION

The dusky dolphin is increasingly threatened by human activities along the Argentine coast,

becoming a vulnerable species in need of a conservation programme. The results of these analyses indicate a strong regional phylogeographic structure for dusky dolphins along the Argentine coast. The spatial genetic analysis suggests the presence of two genetically differentiated groups, corresponding to Buenos Aires, Golfo San Matías, Golfo San José, Golfo Nuevo, Golfo San Jorge vs. Ushuaia. Dusky dolphin groups distributed along the continental shelf are isolated from insular groups. Nevertheless, Ushuaia, at the southern end of the species distribution in the Argentine Sea, is represented by only one individual. However, it does represent a unique haplotype, and thus could signify a genetically different group, since this is the first genetic study of the species including samples from this area. In order to further extend the inferences, it would be necessary to expand the sample size. The strong regional phylogeographic structure for dusky dolphins along the Argentine

coast probably represents strong female philopatry and gene flow mediated by males. In mammals, generally females tend to be more philopatric while males tend to disperse more (Greenwood, 1980).

Understanding the behavioural, environmental, and ecological features that underpin population substructure is a prerequisite to the effective use of genetic data in assessing population status and connectivity (Lowther *et al.*, 2012). Dusky dolphins occur all along the continental shelf of Argentina, and are subject to different anthropogenic pressures throughout their distribution. In Buenos Aires province and in Golfo San Jorge they are affected by fisheries (Crespo *et al.*, 1994, 1997, 2000), and high levels of incidental mortality of dusky dolphins have been reported. Incidental mortality in mid-water trawls off Patagonia in the mid-1980s was estimated at 400–600 dolphins per year, primarily females, declining to 70–215 in the mid-1990s (Dans *et al.*, 1997). Several hundred continue to die each year in various types of fishing gear off Argentina (Crespo *et al.*, 2000). A potential increase for anchovy fishing effort is ever present and if this was to occur, the population may not be sustainable (Dans *et al.*, 2003). All dusky dolphin samples from the Golfo San Jorge region came from bycatch by the mid-water trawl fishery that is concentrated in this region. Loizaga de Castro (2013) found this population has unique matrilines, i.e. mtDNA haplotypes only present in the San Jorge population. The distribution of haplotype frequencies observed in the gulf could indicate that some maternal lineages are more prone to bycatch and there is a clear sex bias in Golfo San Jorge samples, with most of them corresponding to mother and calf pairs. Therefore, only a specific proportion of the population is being affected and this could indicate that some maternal lineages may be suffering differential fishing mortality, especially considering that matrilineal groups can move together and be affected by similar phenomena (Baker *et al.*, 1994; Weinrich *et al.*, 2006). If the fishery continues and mitigation or regulation is not enforced, the population is very likely to lose genetic diversity and the viability of the population may be affected, as females of reproductive age are being

caught incidentally. Mendez and colleagues (2008, 2010) studying the Franciscana dolphin, *Pontoporia blainvillei*, off the Buenos Aires coast, found that groups of mothers with calves are more susceptible to bycatch and consequently are losing genetic diversity. They proposed that the joint entanglement of mother–offspring or reproductive pairs, compared with random individuals, might exacerbate the demographic consequences of bycatch, and the loss of groups of relatives means that significant components of genetic diversity could be lost altogether and by-catch could be more detrimental than previously considered (Mendez *et al.*, 2010).

At more local scales, Golfo Nuevo dolphin-watching is a new tourist activity that started in 1997. The short-term changes in behaviour brought about by these activities may have long-term effects on populations, e.g. migration of animals from their habitat, decrease in survival and reproduction (Bejder *et al.*, 2006a, b). Boat effects on feeding behaviour may exert energetic costs on dolphins and reduce an individual's survival and reproductive capacity or maybe associated with shifts in distribution (Dans *et al.*, 2012). Coscarella *et al.* (2003) and Dans *et al.* (2008) evaluated the effect of tour vessels on the behavioural budget of dusky dolphins. Results of these studies showed that feeding behaviour and energy budget are affected by presence of tour boats. Therefore, several sources of perturbation may be stressing this population and management tools are urgently needed.

In cetaceans, some molecular studies support the female philopatry with male dispersal hypothesis (Escorza-Trevino and Dizon, 2000; Möller and Beheregaray, 2004). The dusky dolphins showed an aggregated distribution at a fine geographical scale; the autocorrelation analysis showed that dolphin groups are genetically structured at less than 10 km and are uniformly distributed at 200 km. Therefore, spatial autocorrelation results showed that dolphin groups are not randomly associated and long-term associations are meaningful for this species. Würsig and Bastida (1986) recorded the recapture of two dusky dolphins tagged in the San José Gulf in the 1970s, seven years later off the coast of Mar del Plata, Buenos Aires, 780 km away, and proposed

long-term associations between individuals and large dispersal capacities for the species. Dusky dolphins also show marked seasonal changes in group size and composition (Degrati *et al.*, 2008). The occurrence of mother–calf pairs during the summer only suggests a seasonal pattern of births; during the spring and summer breeding season, females with newborn calves may segregate to reduce the risk of predation (Norris, 1994; Heithaus, 2001; Heithaus and Dill, 2002) or to avoid hostile interactions with conspecifics (Patterson *et al.*, 1998). At the same time, aggregations of smaller groups – sometimes into collections of hundreds of dolphins – may reflect the spatial distribution of prey (Wilson and Richards, 2000) as well as behavioural adaptations for herding and capturing prey (Würsig and Würsig, 1980). Therefore, dusky dolphin group sizes vary in response to reproductive cycle and distribution of prey, and are likely be reconditioned or altered by dolphin-watching activities or fishery bycatch. This effect may be particularly damaging to mother–calf pairs because of the extreme energetic needs of nursing mothers (Dans *et al.*, 2008; Degrati *et al.*, 2008). Off Kaikoura, New Zealand, mother–calf pairs of dusky dolphins are often found in small groups, termed 'nursery groups'. These groups may help protect vulnerable calves from hazards associated with males seeking mating opportunities, predation by sharks or killer whales, and boat traffic (Weir *et al.*, 2008). Conservation management relies on the development of robust, effective population management units (MU) which typically requires the delineation of discrete genetic groups (Moritz, 1994a, b). Evidence for the effects of habitat specialization on population sub-structuring is growing (Geffen *et al.*, 2004; Pilot *et al.*, 2006; Clark *et al.*, 2008; Lowther *et al.*, 2012). These results indicate that at less than 50 km dusky dolphins are strongly aggregated, thus it is possible to define an operational unit to conserve and manage dusky dolphins at this geographical scale. This result can be taken as an indicator at which scale genetic diversity can be conserved with maximum efficiency at minimum cost. This critical distance obtained during this study can be used to define units and to establish strategies for conservation and management programmes. The genetic characteristics of the dusky dolphin should be considered when generating management and conservation tools in particular in each local unit. This study recommends and also encourages managers and NGOs to monitor at the fine scale level and focus efforts on this vulnerable group of dusky dolphin populations by protecting their preferred coastal shallow habitat. Long-term studies are now needed to monitor changes in genetic diversity within and between areas over time, and assess the effects of anthropogenic stress (bycatch, tourism) and climate change in the dusky dolphin's populations along the Argentine coast.

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