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Home sweet home: social dynamics and genetic variation of a long-term resident bottlenose dolphin population off the Chilean coast

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Coastal resident and pelagic nonresident bottlenose dolphins, *Tursiops truncatus*, have been described in north-central Chile. Using long-term residence data (over 13 years of photo-identification) and genetic mtDNA information, we analysed the social dynamics through time and the genetic variation of this long-term resident population, and evaluated its sociogenetic interaction with nonresidents. Pelagic nonresident dolphins exhibited a higher level of genetic diversity than coastal residents and a significant difference in genetic structure was detected between them. Based on the difference in haplotype numbers and frequencies between resident and nonresident populations and between resident males and females, we propose a population dynamic model in which the resident population is composed of (1) resident females (founder lineages) and some of their female descendants that were born in and remained in the group, without effective female immigration from the nonresident population, (2) resident male descendants of the founder lineage that were born in and remained in the group and (3) resident males that were incorporated from the pelagic groups. Male-biased migration from nonresident pelagic groups into the resident population likely contributes to genetic variation and therefore may help limit inbreeding in the resident population. Finally, we propose that the peripatric model of population differentiation, where resident groups are sporadically connected to the pelagic population, may explain the origin of this unique resident population of bottlenose dolphins along the Chilean coast.

Understanding the drivers and implications of animal movements have become fundamental due to their influence on population dynamics and structure (Gilliam & Fraser, 2001; Nathan et al., 2008). At the population level, movement patterns can be generally classified into three broad categories: resident, migratory and nomadic. (1) Resident, or sedentary, refers to individuals that reside in relatively small home ranges or territories, compared to the population's range (Roshier & Reid, 2003). (2) Migration is defined as a cyclic, regular long-distance pattern of movement to and from breeding and nonbreeding grounds (Roshier & Reid, 2003) and (3) nomadism denotes individuals moving along routes that vary widely or from season to season, and do not repeat annually (Mueller & Fagan, 2008). Such movements are unpredictable and are generally associated with resources that fluctuate irregularly on a multiyear scale over large geographical areas. These three categories are not mutually exclusive, meaning more than one of these patterns may occur within or among populations of the same species (e.g. Hundertmark, 1998) at the same time or at different times (Jahn, Levey, & Smith, 2004).

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Each of these movement strategies is represented within the Cetacea. The most widely studied migrant baleen whale species are the humpback whale, *Megaptera novaeangliae*, and the grey whale, *Escrhictius robustus*, however, most baleen whales are potential migrants (Forcada, 2009). Resident strategies have been reported mainly in toothed whales (here after odontocetes) including *Cephalorhynchus* dolphins (Dawson & Slooten, 1988; Hamner, Pichler, Heimeier, Constantine, & Baker, 2012; Heinrich, 2006; Oremus et al., 2012; Pérez-Alvarez, Alvarez, Aguayo-Lobo, & Olavarría, 2007; Pérez-Alvarez et al., 2015), the Amazon river dolphin, *Innia geoffrensis* (da Silva, 2009), bottlenose whales (*Hyperodon* spp.: Gowans, 2009) and the vaquita, *Phocoena sinus* (Hohn, Read, Fernandez, Vidal, & Findley, 1996). Resident dolphins tend to live in relatively small groups in protected inshore habitats. They do not range widely, probably due to the reliability of food resources. Individuals or small groups are likely better able to avoid predators than are larger groups (Gowans, Würsig, & Karczmarski, 2008). Finally, the nomadic strategy has been described for pelagic species, mainly odontocetes that travel long distances in search of food. They are often in large groups of hundreds to thousands, which may help with the detection of prey and predators (Olson, 2009). Because of the difficulty of collecting data such as photo-identification and genetic samples (Gowans et al., 2008), little is known about the population structure of these wide-ranging offshore cetaceans. It is suggested that these dolphins feed on sparsely distributed abundant food, thus reducing competition (e.g. *Stenella longirostris*: Andrews et al., 2006; Gowans et al., 2008; Karczmarski, Würsig, Gailey, Larson, & Vanderlip, 2005). Smaller *Delphinus* spp. tend to move in very large groups, while larger species such as Risso's dolphins, *Grampus griseus*, and the false killer whales, *Pseudorca crassidens*, tend to occur in smaller schools (Gowans et al., 2008). The largest odontocete, the sperm whale, *Physeter macrocephalus*, also appears to be a nomadic species and shows wide movements between areas of concentration (Mizroch & Rice, 2013; Whitehead, Coakes, Jaquet, & Lusseau, 2008).

While a specific movement strategy has been clearly identified for some species or populations, others show a mixture of strategies. For example, some populations of pilot whales (*Globicephala* spp.) and spinner dolphins (*Stenella* spp.) have been described as nomads (Gowans et al., 2008; Olson, 2009), while others have been identified as resident populations (*Globicephala* spp. off the California coast and Hawaii; Olson, 2009), remaining philopatric and showing a complex network of social interactions (e.g. *Stenella* spp.: Karczmarski et al., 2005). Both resident and transient groups have also been described for killer whales, *Orcinus orca*. Resident killer whales form relatively large, closely related groups and forage predominantly on individual or schooling fishes. These groups range less widely than transient killer whales. Transient killer whales feed on marine mammals and form smaller groups in order to hunt their prey cooperatively. These two 'ecotypes' are morphologically, ecologically and genetically distinct populations and maintain social and reproductive isolation (Ford et al., 1998).

The bottlenose dolphin, *Tursiops truncatus*, also shows a mixture of movement strategies. It has a cosmopolitan distribution and inhabits both coastal and oceanic habitats of temperate and tropical waters. This species exhibits a wide range of intraspecific variation in ranging patterns (Bearzi, Saylan, & Hwang, 2009; Wilson, Thompson, & Hammond, 1997). In some populations, individuals are year-round residents, staying within a small home range (e.g. 15–65 km^2; Gubbins, 2002) and living in the same area for many years or for their entire life (Connor, Wells, Mann, & Read, 2000). For example, in Sarasota Bay, Florida, U.S.A., approximately 100 dolphins resided in an area of about 125 km^2 for at least 30 years (Wells, 2003). Other resident populations, with group sizes generally of tens of individuals, have been described in Texas, U.S.A. (Irwin & Würsig, 2004), Moray Firth, Scotland (Wilson et al., 1997), Shark Bay (Smolker, Richards, Connor, & Pepper, 1992) and Moreton Bay, Australia (Chilvers & Corkeron, 2001) and Fiordland, New Zealand (Lusseau, 2005).

In contrast, other larger groups of *T. truncatus* populations (mostly composed of hundreds of individuals) are nomadic with little or no site fidelity (Ballance, 1992; Defran & Weller, 1999). These groups exhibit a low level of genetic structure and are generally considered as a single genetic unit over a large geographical distance (Quérouil et al., 2007; Tezanos-Pinto et al., 2009). In this context, two 'ecotypes' have been described by Duffield, Ridgway, and Cornell (1983) as 'inshore/coastal' and 'offshore/pelagic' nomadic types, based on haematology profiles and distribution. Later studies confirmed this finding with independent lines of evidence from morphology, genetics, parasite load and diet (Hersh & Duffield, 1990; Hoelzel, Potter, & Best, 1998; Mead & Potter, 1990; Natoli, Peddemors, & Hoelzel, 2004). In particular, genetic differentiation has been detected systematically between resident and nonresident populations , while coastal populations exhibit much lower levels of genetic diversity compared to adjacent pelagic groups (Natoli et al., 2004). Based on the social and genetic conformation of resident populations, it has been proposed that pelagic populations are likely to be the source of independent founder events that have generated resident populations in coastal areas (Hoelzel et al., 1998; Natoli et al., 2004). However, there has been a lack of empirical data to test this hypothesis, to evaluate interactions between resident and nomadic populations, or to explain how these populations persist over time.

In Chile, numerous nomadic groups of *T. truncatus* are sighted along the entire coastline and follow the general pattern described worldwide (Aguayo-Lobo, Torres, & Acevedo, 1998; Olavarría et al., 2010). However, a single resident population has been reported in north-central Chile, in a small area between the Isla Chañaral Marine Reserve and the Choros-Damas Marine Reserve (29°02′–29°14′S). In this zone, long-term studies show that sympatric resident and transient bottlenose dolphins differ in behaviour, group size and site fidelity (Santos-Carvallo et al., 2018; Thomas, 2005). Some resident individuals show long residence (≥15 years) and strong site fidelity, using the area for feeding, nursing and calving, and 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 (Santos-Carvallo et al., 2018).

In this study, using long-term residence data from a 13-year systematic photo-identification study of the resident population and genetic mtDNA information from both the resident and nonresident dolphins, we analysed the social dynamics over time and the genetic variation of a long-term resident bottlenose dolphin population off the central coast of Chile, and evaluated its sociogenetic interaction with nonresident groups. We hypothesize a contribution of genetic variability from the pelagic nonresident group to the coastal resident group as an underlying mechanism that may permit the resident group's persistence over time.

METHODS

Study Area, Data Collection and Residence Categories

A systematic long-term monitoring programme of *T. truncatus* within the Isla Chañaral (29°02′S, 71°36′W) and Choros-Damas (29°14′S, 71°32′W) Marine Reserves was undertaken from 2003 to 2015, with a gap of 3 years (2011–2013; Table 1). A total of 95 boat-based surveys were conducted (Fig. 1), using a 7 m local

Table 1
Annual sightings of photo-identified resident *T. truncatus* at Isla Chañaral and Choros-Damas Marine reserves between 2003 and 2015

ID	Sex	2003	2004	2005	2006	2007	2008	2009	2010	2014	2015	Res (years)	Hap
1		1	1	1	1	1	1	1	1	1	1	10	
2	M	1	1	1	1	1	1	1	1	1	1	10	H1
3	M	1	1	1	1	1	1	1	1	1	1	10	H1
4		1	1	1	1	1	1	1	1	1	1	10	
5	M	1	1	1	1	1	1	1	1	1	1	10	H13
6		1	1	1	1	1	1	1	1	1	1	10	
7	M	1	1	1	0	1	1	1	1	1	1	9	H4
8	M	1	1	1	1	1	1	1	0	1	1	9	H1
9	F	1	1	1	0	1	1	1	1	1	1	9	H1
10	F	1	1	1	0	1	1	1	1	1	1	9	H1
11	M	1	1	1	0	1	1	1	1	1	1	9	H1
12	F	0	1	1	1	1	1	1	1	1	1	9	H4
13	M	1	1	1	1	1	1	1	0	1	1	9	H4
14	M	1	1	1	1	1	1	1	1	0	0	8	H23
15	F	1	1	1	1	1	1	1	1	0	0	8	H1
16	F	1	1	1	0	1	1	1	1	0	0	7	H1
17	F	1	1	1	0	1	1	1	1	0	0	7	H4
18	F	1	1	1	0	1	1	1	0	0	0	6	H1
19	F	0	1	1	1	1	1	1	0	0	0	6	H1
20	M	1	1	1	0	1	1	1	0	0	0	6	H4
21	M	1	1	1	1	1	1	0	0	0	0	6	H1
22	F	1	1	1	0	1	1	1	0	0	0	6	H7
23	M	1	1	1	0	1	1	1	0	0	0	6	H22
24	F	0	0	0	1	1	1	1	1	0	0	5	H2
25		0	0	0	0	0	0	1	1	1	1	4	
26	M	0	0	1	1	1	0	0	0	0	0	3	H1
27	M	0	0	0	0	0	0	0	0	1	1	2	H1
28		0	0	0	0	0	0	0	0	1	1	2	
29		0	0	0	0	0	0	0	0	1	1	2	
30		0	0	0	0	0	0	0	0	1	1	2	
31	M	0	0	0	0	0	0	0	0	1	1	2	H1
32	M	0	0	0	0	0	0	0	0	1	1	2	H1
33	F	0	0	0	0	0	0	0	0	1	1	2	H1
Surveys		6	11	11	10	7	7	6	5	5	5		

ID: individual identity; Sex: genetically identified females (F) and males (M); 2003–2015: years of surveys; Res (years): number of years each individual was resighted; Hap: mtDNA (Dloop) haplotype code for each individual; surveys: number of surveys per year. Sex and haplotype code are not shown for photo-identified individuals that were not genetically sampled.

fishing vessel equipped with a 40 hp outboard motor. Surveys were carried out at least four times per year during daylight hours from 0700 to 1700 hours in Beaufort Sea States of 3 or less. During each survey, a visual examination of the area was undertaken by at least three experienced observers with the naked eye and binoculars. In the presence of dolphins, the boat approached them at a constant speed following the protocol of Würsig and Jefferson (1990).

Photographs of dorsal fins were taken perpendicular to the body axis by at least two researchers, as suggested by Würsig and Jefferson (1990) using Canon 30D and 40D digital cameras equipped with 70–200 mm and 100–400 mm autofocus zoom lenses. In the laboratory, photographs were first assessed for quality (focus, clarity, contrast, angle, dorsal fin position) using Adobe Photoshop CS2 imaging software, and the best quality photographs were selected for analysis following Stevick, Palsbøll, Smith, Bravington, and Hammond (2001). Quality selection of photographs helped reduce the rate of error and eliminate bias from overrepresentation.

Individual dolphins were identified by natural markings such as nicks and notches on both the trailing and leading edges of the fin. A photo-identification catalogue of all resident bottlenose dolphins in the study area was initiated in 2003 and updated throughout the study period. Photographs from each encounter were visually compared with all individuals in the catalogue by two experienced researchers, using Windows Photo Gallery and Adobe Photoshop Lightroom (v.2.7) imaging software to determine whether individuals were present in the existing catalogue or were new additions (Würsig & Jefferson, 1990). Unmarked (nonidentifiable) individuals were also photographed but were not included in the catalogue.

Residence categories

We used two residence categories for this study.

(1) The resident group was defined as dolphins that used the area for feeding, nursing and calving and formed small groups of 2–25 individuals (Segura, Rocha-Olivares, Flores-Ramírez, & Rojas-Bracho, 2006). This category was composed of (a) individuals that had been individually identified in multiple years since 2003 (Table 1) and (b) unidentified dolphins, typically juveniles or subadult individuals, that could not be monitored through time because of the absence of identifiable marks. Some of these individuals likely became part of an identifiable group, as they gained individually identifiable marks.

(2) The nonresident pelagic group was defined as those seen in larger groups (more than 70 individuals; range 5–500) that used the area mainly as a corridor for travelling (Santos-Carvallo et al., 2018).

These two residence categories correspond to ecotypes that show phenotypic differences, mostly in dorsal fin shape and colour, which simplifies visual differentiation, especially among adult individuals (Mead & Potter, 1990).

Genetic Sampling

Skin samples were obtained from free-swimming dolphins by biopsy darting (Harlin, Würsig, Baker, & Markowitz, 1999) and stored in 90% ethanol. To avoid resampling individuals, the nonmarked (unidentifiable) dolphins were only sampled in the last two years of the study (2014 and 2015) and visual monitoring of each sampled individual was implemented during the sampling surveys.

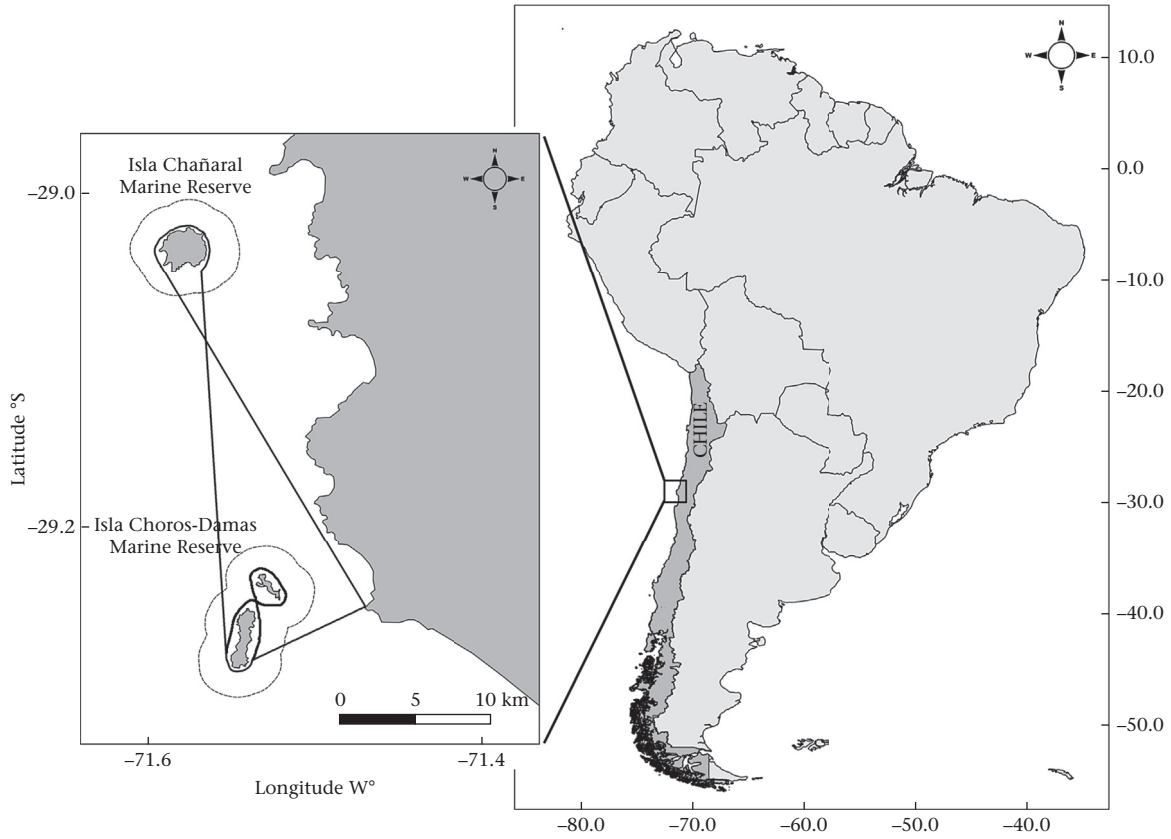

Figure 1. North-central coast of Chile where both long-term residence information and genetic samples of *Tursiops truncatus* were obtained. The line exemplifies a boat sampling route within the entire study area.

For analysis, the integration of genetic information (sex and haplotype) helped to minimize repetition of the same individuals in our data.

Sex Identification and Mitochondrial DNA Sequencing (Dloop)

DNA extraction followed the salt extraction method (Aljanabi & Martinez, 1997). The sex of each individual was identified simultaneously using two sets of oligonucleotide primers, which amplify a fragment of the *ZFX/ZFY* genes (Aasen & Medrano, 1990) and a fragment of the *SRY* gene (Gilson, Syvanen, Levine, & Banks, 1998). Sex identification runs were performed two to three times per individual and a positive control (individual of known sex) was used to corroborate sex identification.

A 750 base pair (bp) fragment of the mitochondrial DNA control region (Dloop) was amplified for 66 individuals using the primers M13 Dlp1.5 5′-TGTAAAACGACAGCCAGTTCACCCAAAGCTGRARTTCTA-3′ and 8G 5′GGAGTACTATGTCCTGTAACCA-3′ (Dalebout et al., 2005). Amplification reactions were performed in a total volume of 25 µl, with 12.7 µl of water, 5 µl of 10X PCR buffer (Invitrogen), 2 µl at 50 mM of MpgCl2 (Invitrogen), 1 µl at 10 mM of each primer and 2 µl at 1 mM of dNTP mix (Invitrogen). Per reaction volume, we used 1.5–2 units of Taq DNA polymerase (Invitrogen) and 50 ng of DNA. All concentrations represent final/working concentrations. The PCR temperature profile was as follows: a preliminary denaturation period of 2 min at 94 °C followed by 30 cycles of denaturation for 30 s at 94 °C, primer annealing for 40 s at 56 °C and polymerase extension for 40 s at 72 °C, with a final extension period of 10 min at 72 °C.

Forward and reverse strands were sequenced using an ABI 3730XL Analyzer by Macrogen (Seoul, South Korea). Sequences were edited and aligned in PRO-Seq 2.91 (Filatov, 2002) and the species was confirmed using a basic local alignment search tool (BLAST) in GeneBank and by DNA Surveillance (Ross et al., 2003). Because sequences obtained previously from the oldest skin samples (obtained in 2009) were only 382 bp long, sequences were trimmed to this length.

Genetic Diversity and Differentiation

We investigated genealogical relationships of the haplotypes by constructing a median-joining network in Network v.4.5.1.0 (Röhl, 2002). Genetic diversity indices were estimated using Arlequin v.3.5 (Schneider & Excoffier, 1999) for both resident and nonresident groups: number of haplotypes (Hap_N), allelic richness (Hap_r, number of haplotypes after rarefaction), haplotype diversity (h, calculated from haplotype frequencies) and nucleotide diversity (π, calculated from pairwise nucleotide differences). Allelic richness (Hap_r) was calculated using the rarefaction method based on the smallest sampling size (residents) with 1000 randomization steps using Past (Hammer, Harper, & Ryan, 2001). We evaluated the genetic difference between resident and nonresident populations by performing exact tests in Arlequin v.3.5 (Excoffier, Laval, & Schneider, 2005). We tested the hypothesis of a random distribution of k haplotypes among r populations using an exact test of population differentiation in Arlequin. This test is analogous to a Fisher's exact test on a 2×2 contingency table extended to a $r \times k$ contingency table (Raymond & Rousset, 1995).

RESULTS

Sighting History of Identified Resident Bottlenose Dolphins

Thirty-three individuals were identified during the 2003–2015 surveys and were resighted over spans of 2–10 years. Among these,

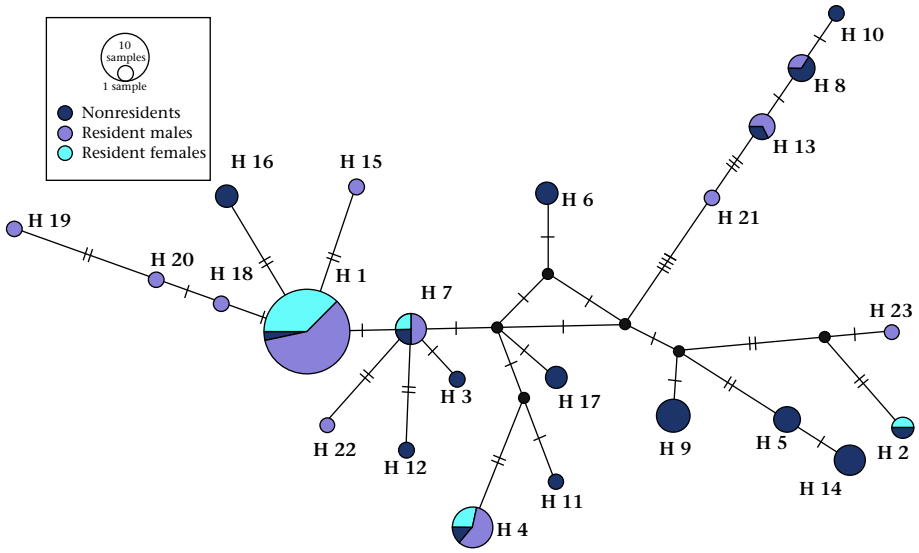

Figure 2. Median-joining network of mtDNA control region haplotypes of *Tursiops truncatus* off the north-central coast of Chile. Circle size is proportional to the number of individuals sharing a haplotype. The number of mutational steps separating haplotypes is depicted by the number of hatch marks on the lines connecting them.

12 were continuously sighted within the study area, while the others ($N = 21$) were identified during the study and/or disappeared before 2015 (Table 1).

Genetic Sampling and Sex Identification

From 2009 to 2015, we collected a total of 80 tissue samples from 52 resident ($N = 26$ photo-identified, $N = 26$ unidentifiable) and 28 nonresident pelagic *T. truncatus* dolphins in the study area. During the entire study period, we recorded a maximum of 35 individuals in the study area at one time (during 2014).

Sex was successfully identified in 76 of 80 sampled dolphins. No conflicting results on sex identification were found between replicate PCRs of the same samples. The overall sex ratio did not differ from the expected 1:1 ($N = 76$: 41 males, 35 females; two-tailed exact binomial test: $P = 0.56$), however, the sex ratio was biased towards males in the resident population ($N = 50$: 35 males, 15 females; two-tailed exact binomial test: $P = 0.006$) and towards females in nonresident groups ($N = 26$: 6 males, 20 females; two-tailed exact binomial test: $P = 0.009$).

Genetic Diversity and Maternal Founder Lineages (mtDNA)

All dolphin samples ($N = 80$) were successfully amplified for mtDNA control region, with a high-quality (HQ) record over 97% after trimming, as measured with Geneious (Kearse et al., 2012). We identified a total of 23 mtDNA haplotypes across the 80 samples. We estimated a haplotype diversity (h) of 0.83 ± 0.05 and a nucleotide diversity (π) of $1.2 \pm 0.003\%$ for all individuals (Table 1, Fig. 2). Four haplotypes were shared between resident and nonresident groups (Fig. 2). Although there were almost twice as many resident samples ($N = 52$) as nonresidents samples ($N = 28$), the residents showed lower genetic diversity indices (13 haplotypes: $h = 0.63 \pm 0.05$; $\pi = 0.08 \pm 0.05\%$) than nonresidents (16 haplotypes: $h = 0.95 \pm 0.03$; $\pi = 0.14 \pm 0.07\%$). This was particularly clear based on the number of haplotypes after rarefaction correction, which adjusts for small sample sizes and potential incomplete sampling of haplotypes (residents: 8.34 ± 1.4 haplotypes; nonresidents: 16 haplotypes).

Within the resident population, females ($N = 16$) shared only four haplotypes and had low genetic diversity ($h = 0.44$; $\pi = 0.06\%$; Table 2), whereas nonresident females shared 13 haplotypes ($\text{Hap}_r = 10$) and had higher genetic diversity ($h = 0.94$; $\pi = 1.4\%$). Resident males shared 11 haplotypes and showed higher diversity than resident females ($\text{Hap}_r = 6.45 \pm 0.14$; $h = 0.68$; $\pi = 0.9\%$). Assuming that individuals sharing the same mtDNA haplotype belong to the same maternal lineage, resident males ($N = 35$) were subdivided into groups that either (1) shared haplotypes with the resident females (descendent males, $N = 25$) or (2) showed haplotypes not present among resident females (nondescendent males, $N = 10$). As expected, the 'descendent males' exhibited low diversity with only three haplotypes ($h = 0.41 \pm 0.11$; $\pi = 0.4 \pm 0.2\%$) while the 'nondescendent males' had much higher genetic diversity with nine haplotypes ($h = 0.98 \pm 0.05$; $\pi = 1.9 \pm 0.1\%$) (Table 2).

Genetic Differentiation

We found significant differences in genetic structure between (1) nonresident pelagic and resident coastal groups (exact test: $P = 0.0001$), (2) the nonresident group and resident females (exact test: $P = 0.017$) and (3) resident females and nondescendent males (exact test: $P = 0.003$). In contrast, no genetic differentiation was observed between (4) the nonresident group and nondescendent males (exact test: $P = 0.10$) or (5) resident females and descendent males (exact test: $P = 0.76$). We propose a dynamic population model to explain the population structure of the resident dolphin group (see Fig. 3).

Table 2
Genetic diversity in resident and nonresident *Tursiops truncatus* off the north-central coast of Chile

mtDNA	N	Hap_N	Hap_r	h±SD	π±SD (%)
Nonresidents					
Total	26	16	16	0.95±0.03	1.4±0.7
Residents					
Total	50	13	8.34±1.4	0.63±0.05	0.8±0.5
Females	15	4		0.44±0.14	0.6±0.3
Males	35	11		0.68±0.08	0.9±0.5
Descendent males	25	3		0.41±0.11	0.4±0.2
Nondescendent males	10	9		0.98±0.05	1.9±0.1

Number of samples (N), number of haplotypes (Hap_N), number of haplotypes after rarefaction (Hap_r), haplotype diversity (h), nucleotide diversity (π).

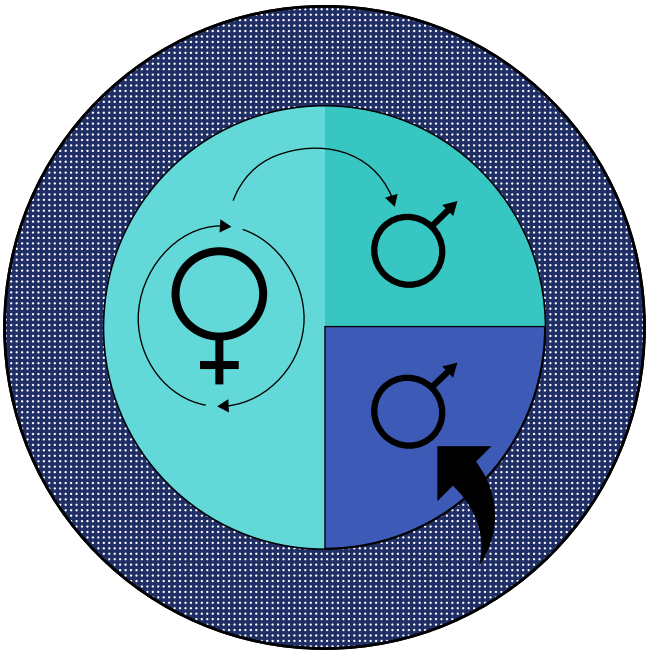

Figure 3. Dynamic population model that explains the population structure and interactions of resident and nonresident bottlenose dolphins, *Tursiops truncatus*. Nonresident pelagic dolphins (dark blue) immigrate into the resident group and join the resident females (light cyan) and their assumed descendants (dark cyan).

DISCUSSION

The findings of this study reveal genetic differences between coastal resident and pelagic nonresident *T. truncatus* populations in north-central Chile. As previously described in other areas worldwide (Caballero et al., 2012; Gaspari et al., 2015; Hoelzel et al., 1998; Natoli et al., 2004; Segura et al., 2006; Sellas, Wells, & Rosel, 2005; Tezanos-Pinto et al., 2009), pelagic *T. truncatus* exhibited higher levels of genetic diversity ($h = 0.95$; $\pi = 1.4\%$) than the coastal resident group ($h = 0.63$; $\pi = 0.8\%$), and highly significant differences in allele frequencies were detected between these groups. The low value of genetic diversity within the resident dolphin group in this study was revealed by the very few mitochondrial lineages shared among resident females and the high frequency of haplotype H1 among both resident females and males. Only three haplotypes were continuously present among resident females throughout the study period; a fourth haplotype was only temporarily present among females (see below). The three permanently present haplotypes might correspond to the maternal founder linage of the resident population. Because of (1) the low frequency of these three haplotypes in the nonresident population ($f_{Hap} < 0.04$) and (2) the high number of haplotypes (Hap = 16) in the nonresident population, it is probable that resident dolphins sharing these three haplotypes correspond to individuals that were born in and remained in the resident population. As has been shown in other studies, it would be worthwhile to consider potential immigration of individuals from other resident groups as a valid alternative (e.g. Möller & Beheregaray, 2004), however, no other resident groups of *T. truncatus* have been reported in the area. In particular, neither our team nor local people have detected another resident group within 140 km of coastline around the study area. Moreover, 'dolphin-watching' tourism activity has been developed only within the confines of our study area, testifying to the permanence and uniqueness of this resident dolphin population.

Among the total 15 resident females reported during the whole study, 14 shared the founder haplotypes and would correspond to founder females or females that were born and remained in the resident population. Between 2003 and 2015, only a single female with a different haplotype (the fourth haplotype belonging to resident females) joined the resident group (ID 24, H2, Table 1). However, this female stayed in the resident group for only 5 years (2006–2010) and did not produce offspring. Thus, the low frequency of the founder haplotypes in the nonresident population and the high number of haplotypes in the nonresident population as well as the lack of new haplotypes among resident females suggest that few, if any, females from the nonresident population were effectively incorporated into the resident population.

Of the 35 resident males observed during our study, 25 shared the three founder haplotypes (Fig. 2), suggesting that these 25 males were born and remained in the resident population. The remaining 10 males showed nine haplotypes that differed from the 'founder lineages' and were absent among the resident females. Two of these haplotypes were shared with nonresident individuals (Fig. 2) while seven were not found elsewhere, probably due to the high genetic diversity detected in the nonresident population. Moreover, these males were similar in terms of genetic diversity to the nonresident pelagic group (Table 2). This suggests that these 10 males joined the resident group as juveniles or adults from the nonresident group.

Thus, in summary, we propose a population dynamic model in which the *T. truncatus* resident population is composed of (1) resident females (founder lineages) and some of their female descendants that were born and remained in the group, without effective female immigration from the nonresident population, (2) some resident male descendants of the founder lineage that were also born and remained in the group and (3) resident males that were incorporated from the pelagic groups.

Regarding sex-biased dispersal, although bisexual philopatry has been proposed for some coastal resident populations of bottlenose dolphins (Connor et al., 2000), our results of likely 10 male migrants and only one female migrant suggest strongly male-biased dispersal from the nonresident to the resident population. Our result is in the line with the findings of Möller and Beheregaray (2004) and Krützen, Barré, Connor, Mann, and Sherwin (2004). As suggested by Fruet et al. (2014), *T. truncatus* resident populations may be vulnerable to inbreeding mainly due to their reduced population size. When population size is small, inbreeding due to genetic drift increases because the number of individuals contributing to each generation is limited. Consequently, average fitness in a small population is expected to decrease from generation to generation as the level of inbreeding (i.e. homozygosity) increases (Keller & Waller, 2002).

In the *T. truncatus* coastal population of Shark Bay, Australia, Frère et al. (2010) detected high levels of inbreeding and demonstrated that inbred females and females with inbred calves showed reduced fitness (lower calving success). These authors also showed that one of the costs of inbreeding is an increase in weaning duration of inbred calves, delaying the next reproductive period. In another study undertaken in the coastal waters of the southwestern Atlantic Ocean, very low levels of genetic diversity (at both the mitochondrial and nuclear levels) in common bottlenose dolphins are a source of concern (Fruet et al., 2014). Although inbreeding depression has not been observed for this population, inbreeding in this small population may be detrimental for long-term fitness and adaptation, and thus to its viability in the long-term (Hale & Briskie, 2007; Spielman, Brook, Briscoe, & Frankham, 2004). In our study, we suggest that the immigration of males from nonresident groups may provide genetic diversity to the resident population and would contribute to limiting

inbreeding. However, it would be necessary to use co-dominant genetic markers to identify immigrants and evaluate their reproductive success with the resident individuals.

Regarding the origin of inshore groups, two main scenarios have been proposed for *Tursiops* dolphins. On one hand, resident populations may exhibit clear differences from nonresident populations in distribution, foraging, parasite load, morphology and genetics (Mead & Potter, 1990). These differences suggest that the resident ecotype may represent a local subspecies or even a different species from the pelagic nonresident species (Kingston & Rosel, 2004) as proposed for *Tursiops* in the Indian Ocean and in some regions of the Pacific Ocean (e.g. *Tursiops aduncus*: Hale, Barreto, & Ross, 2000; Möller & Beheregaray, 2001; Perrin, Robertson, Van Bree, & Mead, 2007). In this context, all connected resident populations would conform to an evolutionary unit differentiated from nonresident populations (Fruet et al., 2017). On the other hand, resident populations may have originated from pelagic populations independently in different ocean basins (Tezanos-Pinto et al., 2009). Thus, population differentiation between coastal resident and pelagic nonresident groups would follow a peripatric model, with pelagic *T. truncatus* being the source of independent founder events that generated resident populations in multiple coastal areas, possibly driven by resource specialization or philopatry (Hoelzel et al., 1998; Natoli et al., 2004). This model has also been proposed for other species such as *S. longirostris* (Andrews et al., 2010) and *Steno bredanensis* (Albertson et al., 2017). In the present study, male-biased dispersal from the pelagic nonresident population to the resident population suggests a connection between these populations and also suggests that the resident population may have originated from the nonresident population, fitting the peripatric model.

Concluding Remarks

This study highlights the utility of integrating long-term individual sighting data from photo-identification surveys with genetic data in order to evaluate social and genetic interactions between resident and nonresident bottlenose dolphins. Our data collected over 13 years suggest that the resident population is formed by resident females (founder lineages) and some of their descendants (females and males), together with males that immigrated from the nonresident group. Such male-biased migration from nonresident pelagic groups into the resident population of bottlenose dolphins likely contributes to its genetic variation and therefore may contribute to limit the inbreeding in the resident population. Finally, we propose that the peripatric model of population differentiation where resident groups are sporadically connected to the pelagic population may explain the origin of the unique resident population of bottlenose dolphins described along the Chilean coast.

Authors' Contributions

M.J.P.A., E.P., R.M. and R.V. conceived the ideas and designed the methodology; M.J.P.A., R.M. and M.S.C. collected the data; E.P., M.J.P.A. and S.K. contributed reagents, materials and analysis tools; M.J.P.A., E.P., R.M., V.S. and S.K. analysed the data; M.J.P.A., E.P. and R.V. led the writing of the manuscript; M.J.P.A., E.P., RV., S.K., V.S., M.S.C., J.G., J.C. and Y.V. contributed intellectually to the interpretation and discussion of results. All authors contributed critically to the drafts.

Data Accessibility

DNA sequences: GenBank accessions MH042231-MH042253.

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