Marine Mammal Science

MARINE MAMMAL SCIENCE, 30(1): 44–63 (January 2014)

DOI: 10.1111/mms.12027

Population genetic structure and taxonomy of the common dolphin (*Delphinus* sp.) at its southernmost range limit: New Zealand waters

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Abstract

New Zealand is the southernmost limit of the common dolphin's (genus *Delphinus*) distribution in the Pacific Ocean. In this area, common dolphins occur in both coastal and oceanic habitats, exhibit seasonal and resident occurrence, and present high morphological variability. Here we investigated the population structure and the taxonomic identity of common dolphins (*Delphinus* sp.) within New Zealand waters using 14 microsatellite loci, 577 bp of the mtDNA control region, and 1,120 bp of the mtDNA cytochrome *b* gene across 90 individuals. We found high genetic variability and evidence of population expansion. Phylogenetic analyses conducted to clarify the taxonomic status of New Zealand common dolphins did not show any clustering reflecting geographic origin or morphotypes. The microsatellite analysis showed genetic differentiation between *Coastal* and *Oceanic* putative populations, while mtDNA revealed significant genetic differentiation only between the *Hauraki Gulf* and other putative groups. Our results suggest that differences in habitat choice and possible female site fidelity may play a role in shaping population structure of New Zealand common dolphins.

Key words: *Delphinus*, common dolphin, population structure, taxonomy, population expansion.

The common dolphin (*Delphinus* spp.) is a widespread marine mammal with a distribution range spanning across the three oceans. It shows high morphological variability to the extent that its taxonomy is still controversial, reinforced by the disagreement found between morphology-based classification and genetic investigations

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(Heyning and Perrin 1994, Rosel *et al.* 1994, Natoli *et al.* 2006, Amaral *et al*. 2012). Especially in cases where the taxonomic classification is still dubious, assessing the genetic population structure across the whole species' geographic range can be of critical importance: it can provide a better understanding of the evolutionary dynamics of the species, and assess the conservation value of peripheral populations (Eckert *et al*. 2008).

New Zealand waters represent the southernmost limit of the common dolphin's distribution. It is generally recognized that populations at the range edges often exhibit lower genetic variability and increased genetic isolation (Sagarin and Gaines 2002, Sexton *et al*. 2009), which may lead to higher vulnerability. Although this pattern has been confirmed across plant and animal species, generalization should not be automatically applied (Eckert *et al*. 2008), especially since the evolutionary processes behind this reduced variability remain poorly understood. It is plausible that peripheral populations maintain substantial genetic variation. They may adaptively diverge from more central populations owing to different selective pressures and reduced gene flow (Lenormand 2002) and may, therefore, play a role in the maintenance and generation of biological diversity (Mayr 1970, Channell and Lomolino 2000).

In New Zealand waters, common dolphins exhibit high variability. They are found in both coastal and oceanic habitats (Neumann 2001*a*, Stockin *et al*. 2008) and morphological variation, observed particularly in body length and pigmentation, exists between common dolphins inhabiting these differing environments (Stockin and Visser 2005, Stockin and Orams 2009). Common dolphins are reported to occur around much of the New Zealand coastline (Webb 1973), although their occurrence appears to be mostly concentrated off the North Island (Stockin and Orams 2009) and is largely seasonal in most regions. The exception is the Hauraki Gulf (Fig. 1), a shallow protected sea on the north east coast of the North Island, where *Delphinus* occurs yearround (Stockin *et al.* 2008), exhibiting a higher level of site fidelity compared with the adjacent waters of the Bay of Plenty (Neumann *et al.* 2002). While the reasons for this remain unclear, it is possible that the high usage of Hauraki waters for feeding (Stockin *et al*. 2009*a*) and nursing purposes (Stockin *et al*. 2008) contribute to this scenario (Stockin and Orams 2009). However, despite the time spent foraging by the dolphins in this region being almost double that in neighboring open coastlines (Neumann 2001*b*, Stockin *et al*. 2009*a*), a previous dietary study of stomach contents suggests common dolphins occupying Hauraki Gulf waters still travel offshore during the night to feed on the deep scattering layer (Meynier *et al*. 2008). However, to what extent this affects population structure, if at all, remains unclear.

In the Atlantic Ocean, short-beaked common dolphins (*D. delphis*) are typically gregarious, highly mobile, and tend to be characterized by limited population structure even at relatively large geographical scales (Amaral *et al.* 2007*a*, Mirimin *et al*. 2009, Viricel *et al*. 2008), when compared to similar delphinids examined from a similar geographical range (*e.g.,* bottlenose dolphins, Natoli *et al*. 2004). By contrast, populations in the Indian and Pacific Oceans have been shown to form distinct units over relatively small spatial scales (Bilgmann *et al.* 2008, Möller *et al.* 2011). While long-beaked common dolphins (*D. capensis*) can be found in large groups in open oceanic waters (Carretta *et al.* 2011), typically within coastal seas they form smaller aggregations (Bernal *et al*. 2003, Cobarrubia and Bolaños-Jiménez 2007). Within the Hauraki Gulf, the group size and water depths in which animals are located are more akin with the long- as opposed to the short-beaked form (Stockin *et al.* 2008).

Several studies have attempted to clarify the taxonomic status of various common dolphin populations worldwide, using both morphological (*e.g*., Amaha

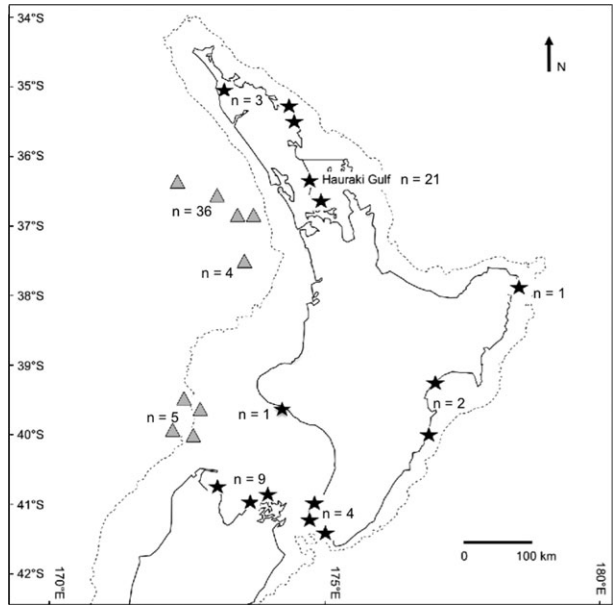

Figure 1. Location of skin samples collected from stranded (stars) and bycaught (triangles) common dolphins (*Delphinus* sp.) in New Zealand waters between 1999 and 2005. Two hundred meters bathymetric profile is reported. More than one sample may be represented by the same symbol. The number of samples is reported for each area.

1994, Heyning and Perrin 1994, Jefferson and Van Waerebeek 2002, Samaai *et al.* 2005, Murphy *et al.* 2006) and molecular (*e.g.*, Rosel *et al*. 1994, Kingston and Rosel 2004, Amaral *et al.* 2007*a*) techniques. However, the reciprocal monophyly observed between the short- and long-beak forms in the eastern North Pacific was not confirmed from worldwide genetic analyses of the genus, suggesting that the long-beaked morphotype may have evolved independently in different regions (Natoli *et al.* 2006, Amaral *et al*. 2012).

To date, no taxonomic assessment has been conducted on New Zealand *Delphinus*, although common dolphins in these waters are nominally classified as short-beaked (*e.g.*, Gaskin 1968, Webb 1973, Slooten and Dawson 1995, Bräger and Schneider 1998, Neumann 2001*a*) based on the apparent absence of the long-beaked form within the South West Pacific (Heyning and Perrin 1994). However, the variation observed in morphological traits such as pigmentation (Stockin and Visser 2005) and skull morphology (Amaha 1994) gives rise to uncertainty. Putative evidence of *D. capensis* is provided by Bernal *et al.* (2003) who suggests that common dolphins exhibiting long rostra, as photographed in New Zealand by Doak (1989), likely represent the long-beaked species. Furthermore, Amaha (1994) and Jefferson and Van Waerebeek (2002) suggest neither New Zealand nor Australian common dolphins fit neatly the morphological description of either *D. delphis* or *D. capensis*.

In this study we aimed to investigate the population structure and the taxonomic status of the New Zealand common dolphin using mitochondrial DNA (mtDNA) sequences and microsatellite markers. We tested for potential population structure of dolphins in New Zealand waters by the examination of three putative groups

(*Coastal*, *Hauraki Gulf*, and *Oceanic*) based on the observation relative to the different habitat use: coastal *vs*. oceanic, and seasonal *vs.* resident.

Materials and Methods

Sample Collection and DNA Extraction

A total of 90 skin samples were collected from common dolphins in New Zealand waters. Of these, 44 samples were collected from stranded or fresh beach-cast carcasses, and a further 46 samples were obtained from common dolphins incidentally captured in the commercial fishery for jack mackerel (*Trachurus* spp.). Samples originating from live stranding or fresh beach-cast events (herein collectively referred to as *stranded*) were collected from around the New Zealand coast between 1997 and 2005. Bycaught samples were obtained from dolphins incidentally killed in mid-water trawls off the west coast of North Island, New Zealand between 2000 and 2004 (Fig. 1). A *fresh* beach-cast was defined as any carcass believed to be less than 24 h old, as determined by the presence of *rigor mortis*, the condition of the skin and the turgor, clarity, and moisture of the eye (Geraci and Lounsbury 1993). Carcasses that exhibited cloudy corneas, dehydrated flaking skin, or that showed any indicators of decomposition were excluded from the present analysis. By using only fresh carcasses, we minimized the possibility of dead oceanic individuals being misclassified when washed ashore. Only adults of both sexes were considered for the analysis in order to avoid the presence of closely related individuals. Adults were defined at post mortem as sexually mature (Stockin *et al*. 2009*b*) or in the absence of the necropsy data, defined as adult if TBL >1.8 m (as per Stockin *et al*. 2008). One mass stranding event was included but related individuals were excluded based on kinship analysis (KAS, unpublished data). Tissue samples were stored in 95% ethanol at −20°C upon collection.

To test for fine scale population structure within the New Zealand sample set, a total of 84 individuals from the 90 samples were selected (six individuals were excluded from the analysis due to their uncertain geographic origin). Specimens were classified into the three putative groups based on origin: *Oceanic* = samples collected from bycaught common dolphins captured in fisheries operating on or beyond the edge of the continental shelf in waters deeper than 200 m (Meynier *et al*. 2008); *Hauraki Gulf* = stranded samples collected from individuals within Hauraki Gulf waters that originally live stranded or were deemed fresh and unlikely to have become washed ashore as oceanic beach-cast; *Coastal* = stranded samples collected from elsewhere around the New Zealand coast that originally live stranded or were deemed fresh and unlikely to have become washed ashore as oceanic beach-cast.

DNA was extracted from tissue samples using a standard phenol/chloroform/isoamyl extraction method (Sambrook *et al.* 1989). An extraction including everything except tissue was carried through all the analyses as a negative control. DNA quality was assessed through visualization under UV light on a 1.5% agarose gel in 0.5 × TBE buffer stained with ethidium bromide. DNA concentration was quantified using a fluorometer.

Sex Determination

The sex of individuals was determined by a multiplex PCR reaction that simultaneously targets the ZFX and SRY genes, as described in Rosel (2003). Individuals of

known sex (confirmed *via* necropsy) were included in each run to serve as positive controls.

Microsatellite Genotyping

All samples were genotyped at 15 polymorphic microsatellite loci: 8 tetranucleotide (Tur4_80, Tur4_87, Tur4_105, Tur4_141, Tur4_142, Tur4_E12, Tur4_F10 (Nater *et al*. 2009) and *Dde* 59 (Coughlan *et al*. 2006) and 7 dinucleotide (*Dde*66, *Dde*70 (Coughlan *et al*. 2006), KWM2, KWM12a (Hoelzel *et al*. 1998), EV1 (Valsecchi and Amos 1996), MK6 and MK8 (Krützen *et al*. 2001)). Amplification reactions contained 50–100 ng DNA, 1 × reaction Promega Taq buffer, 2.5 mM $MgCl_2$, 0.2 mM dNTPs, 0.1 μM of each primer and 1 unit of Promega Taq DNA polymerase. The thermal cycler profile for the tetranucleotide loci and *Dde*66 and *Dde*70 consisted of initial denaturation at 94°C for 3 min followed by a touchdown profile for 5 cycles with initial denaturation at 94°C for 20 s, annealing temperature starting at 63°C and decreasing 2°C per cycle for 45 s and 72°C for 1 min, followed by 30 cycles with the same initial denaturation and final extension temperatures, but an annealing temperature of 53°C, followed by a final extension step at 72°C for 10 min. In each cycle, for the remaining dinucleotide loci, conditions followed the original publications. All reactions included both positive and negative controls. Following amplification, samples were mixed with an internal size standard (LIZ 500) and run on an ABI 3130 Genetic Analyzer. The GeneMapper 4.1 software (Applied Biosystems, Carlsbad, CA) was used for sizing of allele fragments.

Mitochondrial DNA Amplification

The first 577 basepairs (bps) at the 5 end of the mtDNA control region were sequenced in both forward and reverse directions with the primers L15926 and H00034 (Rosel *et al*. 1994). The PCR reaction conditions were as follows: 10–100 ng of DNA, 0.15 mM dNTPs, 1.5 mM $MgCl_2$, 10 mM Tris-HCl pH 9.0, 50 mM KCl, 0.3 μM of each primer, 1.5 U Taq polymerase per reaction. The PCR cycling profile was 35 cycles of 1.5 min at 94°C, 2 min at 45°C, 2.5 min at 72°C, followed by 3 min at 72°C.

A subset of 40 samples, randomly chosen from each of the three putative populations, was further sequenced for the cytochrome *b* gene, in both forward and reverse directions, using conditions described in Amaral *et al.* 2007*b*. These sequences were used to investigate the taxonomic status of New Zealand common dolphins by comparing them with 155 sequences available from different oceans (Amaral *et al*. 2012). The cytochrome *b* gene has been suggested to be more reliable than the control region in species identification in closely related groups such as delphinids (*e.g.,* Amaral *et al*. 2007*b*). PCR products were purified using a QIAquick PCR purification kit (QIAGEN Pty. Ltd.), and sequencing reactions performed using the ABI PRISM BigDye Terminator Sequencing Kit. Ethanol precipitation was performed on the sequencing products and then separated on the ABI PRISM 3730 automated DNA Analyzer. Sequences were visualized and minor edits performed using SEQUENCHER 4.1 (Gene Codes Corporations Inc.). Sequences were aligned using CLUSTAL X (Thompson *et al.* 1997).

Microsatellite Data Analysis

The program Micro-checker v. 2.2.3 (Oosterhout *et al*. 2004) was used to check for the presence of genotyping errors such as scoring errors due to stuttering, large allele dropout or evidence for null alleles. Departures from Hardy-Weinberg equilibrium were tested for each of the 15 microsatellite loci in each population using ARLEQUIN v. 3.5 (Excoffier and Lischer 2010). A Bonferroni correction was implemented to the *P* values. Genepop v. 4.0 (Rousset 2008) was used to test for linkage disequilibrium between all pairs of loci for each population (1,000 dememorization iterations, 1,000 batches, 10,000 iterations per batch). Genetic diversity measures such as mean number of alleles per locus as well as observed and expected heterozygosities for each population were calculated in ARLEQUIN. The program FSTAT (Goudet 1995) was used to estimate another measure of genetic diversity, allelic richness, as well as to assess population differentiation between the putative populations by estimating the fixation index F_{ST}. Bonferroni correction was not applied (Narum, 2006). FSTAT was also used to analyze sex-biased dispersal among putative populations (*Oceanic*, *Coastal*, and *Hauraki Gulf*) by calculating $F_{IS,}$ H_O, H_E, and applying F_{ST} statistics to each sex independently. Jost estimated D_{EST} (Jost 2008) was also calculated as a measure of pairwise population differentiation in SMOGD (Crawford 2010). A principal component analysis (PCA) was performed on a table of allele frequencies using the R packages ade4 (Thioulouse *et al*. 1997) and adegenet (Jombart 2008) as an exploratory analysis to infer population differentiation (Jombart *et al*. 2009).

The program STRUCTURE v.2.3.3 (Hubisz *et al*. 2009) was used to infer population structure by assigning individuals (probabilistically) to clusters without *a priori* knowledge of population units and limits. The algorithm implemented in this program estimates the log-likelihood of the data for a given number of genetic clusters (*K*), under the assumption of Hardy-Weinberg and linkage equilibrium within clusters. We used the admixture model, which assumes that individuals have admixed ancestry. We performed 10 independent runs for each *K* from 1 to 6 using the correlated allele frequency with 1,000,000 repetitions and a burn in of 100,000. The estimated Ln probability for the data was averaged across the runs for each *K*. Structure Harvester (Earl and von Holdt 2012) was used to detect the most likely *K* based on the Evanno method (Evanno *et al*. 2005). Population differentiation was additionally tested using a one level hierarchical analysis of molecular variance (AMOVA) in ARLEQUIN v. 3.5 using 10,000 randomizations, in which the existence of differentiation among the three populations was tested.

Estimates of recent migration rates between putative populations were determined using a molecular assignment program that relies on a nonequilibrium Bayesian approach method through Markov Monte Carlo techniques, as implemented in BAYESASS (Wilson and Rannala 2003). This program estimates asymmetrical rates of migration between populations over the last several generations. The program was run using default settings. Convergence was achieved after 3×10^6 MCMC iterations and a burn in of 1×10^6 steps. Five runs were made and the run in which the log-likelihood had peaked with the highest log-likelihood was chosen.

MtDNA Analysis

MtDNA control region variation was estimated by gene diversity (h) and nucleotide diversity (π) according to Nei (1987), as implemented in ARLEQUIN 3.5 (Schneider *et al.* 2000). The degree of differentiation among pairwise populations was estimated as

F_{ST} and Φ_{ST}, using ARLEQUIN 3.5 (Schneider *et al*. 2000). The most appropriate nucleotide substitution model for the mtDNA control region sequences was determined using MODELTEST 3.7 (Posada and Crandall 1998). Based on the results Tamura-Nei was used as genetic distance model (Tamura and Nei 1993). The levels of statistical significance of F_{ST} and Φ_{ST} were tested using a matrix permutation procedure (1,000 simulations). A one level hierarchical analysis of molecular variance (AMOVA) as implemented in ARLEQUIN 3.5 was also used to test the overall population differentiation.

To infer historical patterns of population growth, a mismatch distribution analysis was performed considering all samples using ARLEQUIN 3.5 (Schneider *et al*. 2000). We used values of τ to estimate of time since expansion using the equation $\tau = 2\mu t$, where μ is the mutation rate for the sequence, and t is the time since expansion. We used two estimates of mutation rate: 1.5×10^{-8} per base/yr (Hoelzel *et al.* 1991, Baker *et al.* 1993), 7×10^{-8} per base/yr (Harlin *et al.* 2003). Neutrality and population equilibrium were tested estimating Tajima's D and Fu's F_s values using ARLEQUIN 3.5 (Schneider *et al*. 2000). A median-joining network was generated to infer phylogenetic relationships among the mtDNA control region haplotypes using the program NETWORK 4.5.0.2 (Bandelt *et al.* 1999; http://www.fluxusengineering.com).

In order to assess the taxonomic status of New Zealand common dolphins, the 40 cytochrome *b* (Cytb) sequences obtained were aligned with 155 haplotypes sampled from short- and long-beaked common dolphin populations from Eastern North and South Pacific (off U.S.A. and east Australia coasts) and from the Atlantic Ocean (off U.S.A., European, and South African coasts) used in Amaral *et al*. (2012) (GenBank accession numbers in Table S1). MacClade v.4.08 (Maddison and Maddison 2011) was used to infer haplotypes. A Bayesian phylogenetic tree was estimated using MrBayes v. 3.1.2 (Huelsenbeck and Ronquist 2001). Sequences from *Tursiops truncatus* and *Globicephala melas* were used as outgroups. Four simultaneous MCMC chains were run for 5 million generations, with trees sampled at intervals of 100 generations. Convergence was assessed by the standard deviation of split frequencies and by the achievement of stationary of the log-likelihood values of the cold chain. The first 5,000 trees were discarded as "burn-in." Modeltest v. 3.7 (Posada and Crandall 1998) was used to infer the best-fitting nucleotide substitution model.

Results

Sex Determination

Sex was determined for all the 90 samples. Of the 84 specimens used in the interpopulation analysis, 28 males and 56 females were molecularly identified, a ratio of 1:2. This ratio was relatively consistent throughout all the putative populations examined (*Oceanic*: 13, 30; *Hauraki Gulf*: 6, 14; *Coastal*: 9, 12).

Population Genetic Analysis of New Zealand Common Dolphins

Genetic variation—In total, 79 individuals (45 from the *Oceanic*, 18 from the *Coastal* and 16 from the *Hauraki Gulf* putative populations) were genotyped for the 15 microsatellite loci. Among the fifteen microsatellite loci analyzed no evidence for linkage disequilibrium was found suggesting that alleles are segregating independently. Two loci (Tur141 and *Dde*59) showed significant deviation from Hardy-Weinberg equilibrium (HWE), which was due to heterozygosity deficiency (Table

S2). Tur 141 was removed from subsequent analyses as it showed deviation in two populations but *Dde* 59 was retained because deviation was only found in one population and no evidence of null alleles or large allele dropout was detected using Micro-checker. In total, 14 loci were retained for further analyses.

Levels of genetic variation for the microsatellite data given by expected and observed heterozygosities, mean number of alleles, allelic richness and F_{IS} are given in Table 1. The *Oceanic* and *Coastal* putative populations showed similar values of variability, being higher than the ones obtained for the *Hauraki Gulf* population. F_{IS} values were statistically significant for the *Hauraki* and *Coastal* populations, which can be due to a Wahlund effect (*i.e.*, the existence of further population subdivision within each putative population; see Discussion).

Ninety samples, from known and unknown locations (see Materials and Methods), were successfully sequenced for the first 577 bps of the mtDNA control region. Out of these, a total of 65 haplotypes were identified (GenBank accession numbers: Table S1), of which 47 (73%) occurred only once. For one sample (WB01-13) a shorter sequence was obtained and therefore excluded from the subsequent analyses. However, this sequence represents a different haplotype, exhibiting two unique mutations at 206 and 288 bps (Fig. S1). Haplotypes were characterized by 80 polymorphic sites, at which there were 72 transitions, 8 transversions, and 4 indel events (Fig. S1). The overall gene and nucleotide diversity for the New Zealand population was 0.991 (SD $\pm$ 0.004) and 0.017 (SD $\pm$ 0.009), respectively. Although Tajima's D was not significant ($D = -1.234$, $P\ [D_{simul} < D_{observed}] = 0.077$), Fuès F_s value was highly negative and significant ($F_s = -24.28$, $P\ [D_{simul} < D_{observed}] = 0$) suggesting population expansion. Moreover, the mismatch distribution analysis (Fig. 2) showed a unimodal distribution, reinforcing the hypothesis that the New Zealand population may have undergone a population expansion. The estimated time of expansion, using our estimated value of $\tau = 8.85$, and based on the two mutation rate estimates, were approximately 511,000 and 110,000 ybp (years before present).

Shared haplotypes between the three putative populations, *Oceanic*, *Coastal*, and *Hauraki Gulf*, were not common, with only one haplotype (KS05-29) present in all three putative populations, and only three shared between two populations (WB04-25; WB02-01; KS05-15) (Fig. S1). A median-joining network was drawn including all the New Zealand mtDNA control region haplotypes and considering the putative population subdivision (Fig. 2). The network shows a complex structure with a central core of missing (unsampled or extinct) haplotypes and no clear clustering based on population origin.

Table 1. Descriptive statistics of genetic variability averaged across 14 microsatellite loci in the putative populations analysed. Note: n = number of samples genotyped; H_E = expected heterozygosity; H_O = observed heterozygosity; N_A = mean number of alleles; A_R = allelic richness; F_{IS} = inbreeding coefficient and * = respective significant level, $P < 0.05$. Standard deviation (SD) is also reported.

Population	n	$H_E \pm$ SD	$H_O \pm$ SD	mean $N_A \pm$ SD	A_R	F_{IS}
Oceanic	45	0.801 ± 0.099	0.759 ± 0.133	11.071 ± 4.665	8.188	0.054
Coastal	18	0.816 ± 0.033	0.723 ± 0.141	8.786 ± 3.704	8.369	0.117*
Hauraki	16	0.781 ± 0.102	0.691 ± 0.142	7.786 ± 2.486	7.681	0.118*
	79	0.799	0.724	9.214	8.079	0.054

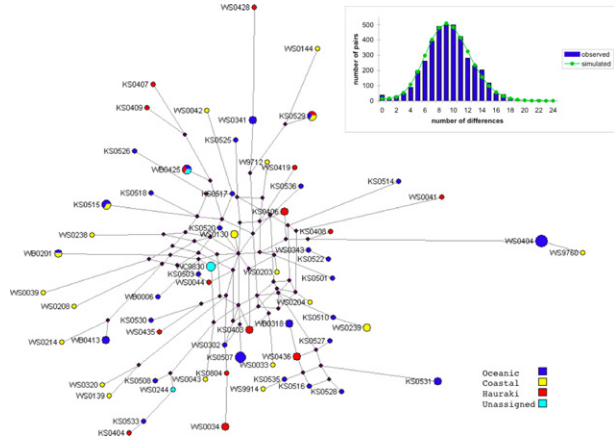

Figure 2. Median-joining network and mismatch distribution (top right) for the New Zealand common dolphin population based on 577 bp of the mtDNA control region. In the graph the observed number of differences is indicated as bars on the histogram and the simulation for an expanding population shown as a green line. In the network, black dots indicate extinct or unsampled haplotypes. The size of the circles is proportional to the total number of haplotypes observed and the length of the branches is proportional to the number of mutations. Sectors are proportional to the numbers of each haplotype observed in each population. Putative populations are represented as follows; yellow indicates *Coastal*, red indicates *Hauraki Gulf*, dark blue indicates *Oceanic.* Light blue indicates haplotypes from individuals whose origin was uncertain.

Population structure—A total of 84 individuals for the mtDNA data set and 79 for the microsatellite data set was examined to test for possible differentiation among putative *Oceanic*, *Coastal*, and *Hauraki Gulf* populations.

The program STRUCTURE was used to test population structure without *a priori* sample assignment to a specific population. The most likely number of clusters was found to be two ($K = 1$, LnP = −4,269.93; $K = 2$, LnP = −4,261.49; $K = 3$, LnP = −4,565.97; $K = 4$, LnP = −4,381.87, $K = 5$, LnP = −4,449.32, $K = 6$, LnP = −4,632.84). The application of the Evanno method also identified $K = 2$ as the most likely number of cluster ($K = 2$, $\Delta K = 70.89$; $K = 3$, $\Delta K = 10.19$; $K = 4$, $\Delta K = 4.45$; $K = 5$, $\Delta K = 2.18$). However, the clusters do not identify any population as previously assigned based on the sample origins (*Oceanic*, *Coastal* or *Hauraki Gulf*) (Fig. 3).

The Principal Component Analysis (PCA) was also performed and the first two principal components explained 64.42% of the total variation (Fig. 4). Along both components, the *Coastal* population appears slightly differentiated from the others.

F_{ST} values, based on the mtDNA data, suggested small but significant genetic differentiation between the putative *Hauraki Gulf*, and the *Coastal* and *Oceanic* populations, although no significant differentiation was detected between the *Coastal* and *Oceanic* groups. Φ_{ST} values did not indicate any significant differentiation (Table 2). The AMOVA analysis indicated 98% of the overall variation due to variance within populations ($Vc = 0.49$, F_{ST} 0.0168, $P = 0.00098$). In contrast, pairwise comparisons of F_{ST} values based on microsatellites showed a small but significant differentiation between *Oceanic* and *Coastal* populations, a result supported by Jost's D_{EST} values

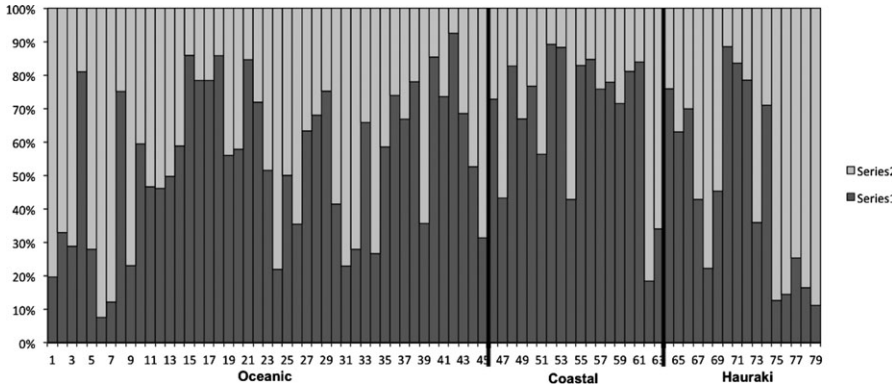

Figure 3. Results from the program STRUCTURE showing individual assignment values for $K = 2$. Each individual is represented by one column. Each color depicts the estimated proportions of the coefficient of admixture of each individual's genome that originated from population K, for $K = 2$. Samples' origin is given below.

(Table 2). However, the result obtained with AMOVA, which gave us an overall estimate of F_{ST}, was not significant ($F_{ST} = 0.00953$, $P = 0.81916$).

When testing for sex-biased dispersal, there was no significant difference ($P > 0.05$) for F_{IS}, F_{ST}, H_E, and H_O between males and females. However, this test is known to have relatively low power, particularly when small sample sizes are used (see Goudet *et al*. 2002). Estimated migration rates, based on microsatellite data, showed lower levels of migration between *Oceanic* and *Coastal* populations in both directions (Table 3), as well as from both *Oceanic* and *Coastal* populations to the *Hauraki Gulf* population, when compared to the higher migration rates observed from the *Hauraki Gulf* population to both *Oceanic* and *Coastal* populations. This suggests unidirectional migration in the latter case. Multiple runs showed consistent results, and the 95% CIs suggested that the data contained sufficient information for reliable migration rate estimates.

Taxonomic Inference of the New Zealand Common Dolphins

In total, 180 Cytb sequences (1,120 bp) were analyzed, including short- and long-beaked common dolphins from the Atlantic and Pacific Oceans. Twenty-five haplotypes were identified amongst the 40 New Zealand common dolphin sequences analysed. No shared haplotypes between New Zealand common dolphins and either short- or long-beaked common dolphins from other regions were found. The Tamura-Nei nucleotide substitution model was the best-fitting model identified by Modeltest for this data set. The Bayesian phylogenetic tree obtained showed several clades strongly supported by high posterior probability values (Fig. 5). However, these clades fail to show any geographical or taxonomic association, with New Zealand common dolphin haplotypes dispersed throughout the tree. Most New Zealand haplotypes clustered with short-beaked common dolphins from the Pacific and Atlantic Oceans, although some clustered with long-beaked common dolphins from eastern North Pacific and from eastern South Atlantic (Fig. 5). Both long-beaked common dolphin populations do not form monophyletic lineages.

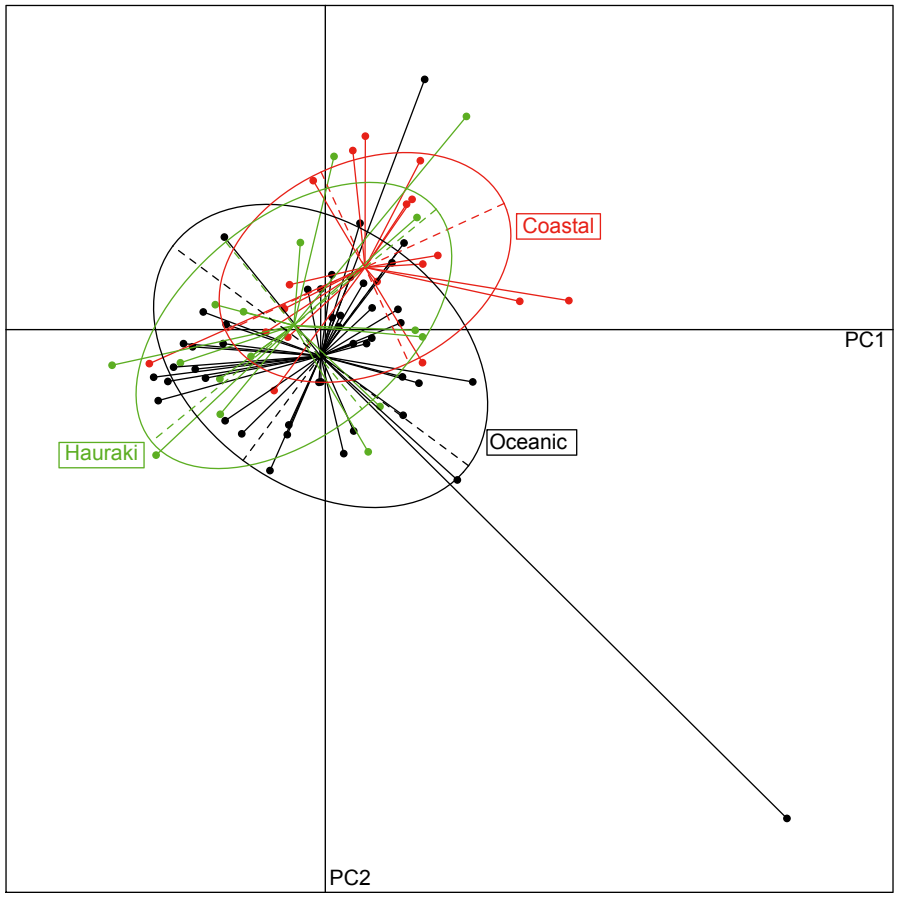

Figure 4. Principal component analysis based on allele frequencies of 14 microsatellite loci.

Discussion

Our results showed high genetic variability among the New Zealand common dolphins at both mitochondrial and nuclear markers, comparable to values reported for other common dolphin populations (Natoli *et al.* 2006, Viricel *et al.* 2008, Mirimin *et al.* 2009, Amaral *et al.* 2012). Both gene and nucleotide diversities based on the mtDNA control region, and H_O and H_E based on the microsatellites were high for the three putative populations considered. Furthermore, throughout their geographic range, *Delphinus* exhibit relatively low genetic differentiation compared to other closely related taxa with similar geographical distribution (*e.g.*, *Tursiops truncatus*; see Natoli *et al.* 2004). This can be expected if we consider that common dolphins are a panmictic species and show high levels of mobility across their habitat (Evans 1971). However, populations residing at the peripheral species' range are generally characterized by lower genetic diversity and higher genetic differentiation (Eckert *et al*. 2008),

Table 2. Genetic differentiation among pairwise New Zealand common dolphin populations using microsatellite and mtDNA control region sequence data. Microsatellite results are reported in the lower matrix, mtDNA results in the upper matrix. "*n*" indicates the number of samples analyzed for each population for each marker. F_{ST} values for both markers are reported in bold and the respective *P* values in parentheses. Jost's estimated *D* distance values for the microsatellites and Φ_{ST} values for the mtDNA are reported in italics. *P* values for the Φ_{ST} were all nonsignificant (>0.05).

	n	Oceanic 43	Coastal 20	Hauraki 21
Oceanic	45	–	**0.01 (0.06)** *0.004*	**0.02 (0.003)** *0.014*
Coastal	18	**0.014 (0.007)** *0.026*	–	**0.011 (0.03)** *−0.003*
Hauraki	16	**0.006 (0.48)** *0.002*	**0.004 (0.14)** *0.005*	–

Table 3. Asymmetric migration rates between putative populations based on the microsatellite data obtained with BayesAss (values are the proportions of individuals derived from the source populations each generation). Confidence intervals are reported in parentheses.

From / To	Oceanic	Coastal	Hauraki
Oceanic		0.0195 (0.0005–0.0712)	0.0139 (0.0001–0.0585)
Coastal	0.0076 (0.0002–0.02893)		0.0182 (0.0002–0.0737)
Hauraki	0.3187 (0.2904–0.3315)	0.2956 (0.2354–0.3287)	

and the pattern observed for the New Zealand common dolphins is more typical of a central population.

Mitochondrial DNA data also provide evidence to suggest that the New Zealand population has undergone expansion, as shown by the neutrality test and the mismatch distribution results. Typically, populations characterized by high levels of haplotypic diversity are large and widely distributed. The high number of unsampled/extinct haplotypes detected by the Network analysis (Fig. 2) may indicate that our sampling failed to sample all the variability present in the population. However, a population expansion event could also offer an alternative explanation to this pattern (Westlake and O'Corry-Crowe 2002). A bimodal mismatch distribution is expected for stable populations, whereas expanding populations produce a unimodal distribution (Rogers and Harpending 1992). The values of the mean and mode of the mismatch distribution are relatively high, suggesting that the expansion may have been an old event. From our estimates, the population expansion would have occurred between 511,000 and 110,000 ybp, coinciding with the middle-late Pleistocene. These estimates concur with the findings reported by Amaral *et al*. (2012). The highly negative Fu F_s value is also supportive of an expansion event (Ray *et al*. 2003).

Our results also suggest that fine scale population structure may occur in New Zealand waters. Small but significant genetic differentiation was observed at both nuclear and mtDNA markers. The fact that differentiation between putative *Coastal*

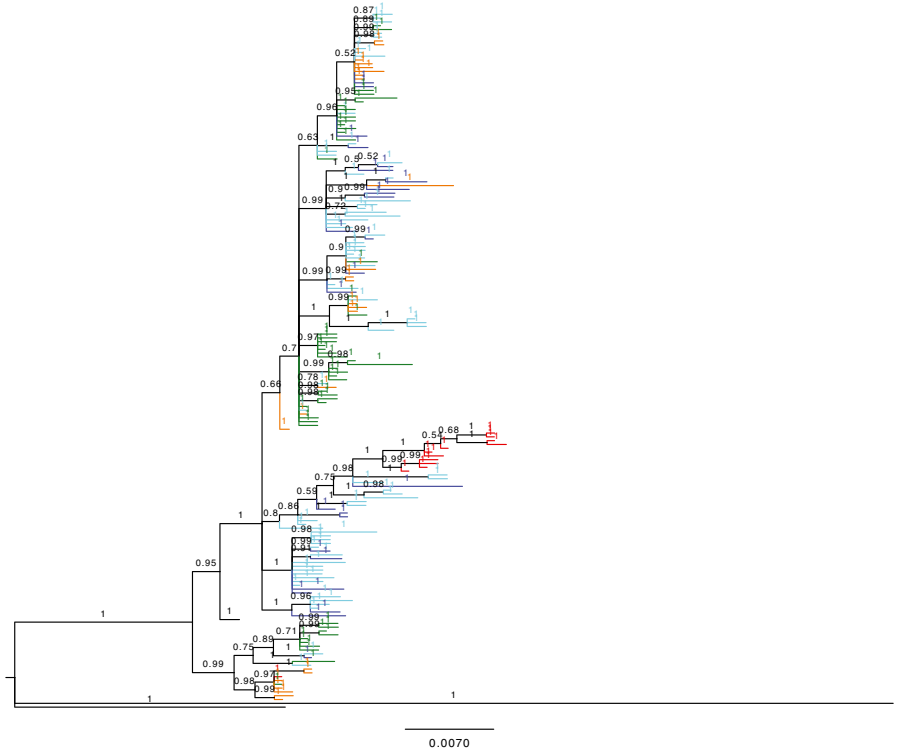

Figure 5. Bayesian phylogenetic tree based on 1,120 bps of the cytochrome *b* and including 180 haplotypes of short- and long-beaked common dolphins from the Atlantic, Pacific Oceans and New Zealand. Colors represent the geographical origin and morphotype: light blue—Pacific short-beaked common dolphins (including Eastern North Pacific and Southwest Pacific); dark blue—NZ common dolphins; green—Atlantic short-beaked common dolphins; orange—Atlantic South Africa long-beaked common dolphins; red—Eastern North Pacific long-beaked common dolphins. Posterior probability values are reported above branches.

and *Oceanic* populations was detected with the microsatellites but not with mtDNA may suggest that these populations have diverged recently. This is supported by the lack of correlation observed between lineages and populations in the median-joining network, but could also be the consequence of a stochastic effect considering the high haplotype diversity. The differentiation of the *Hauraki Gulf* population obtained with mtDNA but not with the microsatellites may be explained by the existence of higher female site-fidelity to this region. Our sex-biased dispersal analysis was too weak to provide reliable results. However, the fact that the Hauraki Gulf retains a notable importance as nursery and feeding ground may support this result (Stockin *et al*. 2008, 2009*a*). Unlike other regions around the New Zealand coast, common dolphins occur in Hauraki Gulf year-round (Stockin *et al*. 2008), with photo-identification suggesting common dolphins exhibit higher site fidelity in this region compared to other neighboring areas (Neumann *et al*. 2002). This behavior has also been observed in another small cetacean species in New Zealand waters (Weir *et al*. 2008). The migration rate estimates showing high directional migration from the *Hauraki Gulf* to the other populations may also help to explain this discrepancy.

These estimates should, however, be considered with caution given the low levels of F_{ST} observed for these populations.

An alternative interpretation of these results is the potential co-occurrence of two distinct populations/ecotypes that do not coincide with an *Oceanic/Coastal* subdivision, as revealed by STRUCTURE. The significant positive F_{IS} values detected in the *Coastal* and *Hauraki* population also suggest some evidence of Wahlund effect, indicating the presence of subpopulations. The dietary differences identified between Hauraki Gulf individuals and other New Zealand common dolphins further suggest that some degree of dietary specialization could occur in this region (Meynier *et al.* 2008). Population structure of short-beaked common dolphins over relatively small spatial scales has been reported in some regions of the Pacific, Indian Oceans, as well as in the Mediterranean Sea (Bilgmann *et al*. 2008, Natoli *et al*. 2008, Möller *et al*. 2011). Divergence between coastal and oceanic forms has previously been noted in several other delphinids including pantropical spotted dolphin (*Stenella attenuata*), Atlantic spotted dolphin (*S. frontalis*) and bottlenose dolphin (*e.g.*, Douglas *et al.* 1984, Dowling and Brown 1993, Lux *et al.* 1997, Hoelzel 1998, Hayano *et al.* 2004, Adams and Rosel 2006). Such divergence has frequently been considered the result of resource heterogeneity (Dowling and Brown 1993, Heyning and Perrin 1994, Hoelzel 1998). Resource heterogeneity is well documented in both terrestrial and aquatic taxa (Smith and Skulason 1996), and relies on individuals of a species specializing in habitat or prey choice. Differential use of habitat has been described for common dolphins occurring off Mauritania, with short- and long-beaked morphotypes exploring different areas (Pinela *et al*. 2011) and occurring in the Bay of Biscay, Northeast Atlantic, with short-beaked common dolphins occupying oceanic and neritic waters (Pusineri *et al*. 2007). The analysis of a higher number of samples from each putative population would assist in assessing sex-biased dispersal and improve our understanding of the fine population structure in this region.

The Bayesian phylogenetic analysis of the cytochrome *b* data set identified well-supported clusters, some of which included New Zealand haplotypes. However, none of the clusters appear to reflect geographic origins or morphotyope. Furthermore, New Zealand common dolphin haplotypes clustered with different clades, including both short- and long-beaked common dolphin haplotypes, leaving the question open as to whether within New Zealand waters, the two forms may coexist. It has been previously suggested that the long-beaked morphotype could have evolved independently in the different ocean basins (Natoli *et al*. 2006, Amaral *et al*. 2012). In the Atlantic Ocean, where populations are more recently evolved, the genetic differentiation between short- and long-beaked morphotypes is still relatively low (Amaral *et al*. 2012). This is clearly observed in the Cytb tree, where both morphotypes cluster together in several clades (Fig. 5). If the long-beaked morphotype is present in New Zealand waters, it may be that these individuals are not yet genetically distinct and are still in the process of differentiation. In addition, niche partitioning can also cause morphological differentiation, as has been recently shown for common dolphins occurring off Mauritania (Pinela *et al*. 2011). This may additionally offer an explanation for the patterns of population genetic differentiation observed for New Zealand common dolphins.

Based on the fact that New Zealand lies at the edge of the distribution range of this species, the studied populations could have been characterized by low genetic variability. Instead, we found high genetic variability and sign of population expansion, supporting the high variability observed in the morphological and behavioral traits of this species in this region. The taxonomic status of the New Zealand common

dolphin has not been entirely clarified, since it is not clear to which lineage it is more related. We also found evidence of population structure suggesting that specialization in habitat or prey choice and site fidelity may play a role in shaping population structure of New Zealand common dolphins.

Acknowledgments

The authors thank staff from the Allan Wilson Centre for Molecular Ecology and Evolution, Massey University, for their assistance with DNA sequencing. Grateful thanks extend to the Department of Conservation, particularly Steph Rowe, Igor Debski, Kris Ramm, Helen McConnell, Steve Smith, and Laura Boren, and additionally to Anton van Helden (Te Papa Museum), Padraig Duignan, Wendi Roe, Laureline Meynier (Massey University), MFISH observers, and DOC rangers for their assistance with carcass recovery and post mortem logistics. Final thanks are owed to Luca Mirimin, Gabriela de Tezanos Pinto, Nicky Wiseman, Mark Orams, and four anonymous reviewers whose useful comments improved earlier drafts of this manuscript. Research permit RNW/HO/2008/03 was issued to KAS by the New Zealand Department of Conservation.

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Received: 30 December 2011
Accepted: 21 December 2012

Supporting Information

The following supporting information is available for this article online at http://onlinelibrary.wiley.com/doi/10.1111/mms.12027/suppinfo.

Table S1. Sequence name, source and GENEBANK accession number of all the haplotype sequences used in this study.

Table S2. P values of the Hardy-Weinberg exact test for each locus in each putative population performed in Arlequin. Significant *P* values after Bonferroni correction ($P < 0.001$) are highlighted in bold.

Figure S1. Polymorphic sites across 577 bp of the mtDNA control (D-loop) region of common dolphins (*Delphinus* sp.) in New Zealand waters. Sixty-four haplotypes are

identified and a shorter haplotype (WB01-13) reported at the bottom of the alignment. Haplotypes names are reported on the left. Dots indicate identity with the reference sequence. Total frequency for each haplotype and haplotype frequency for each putative population (*Oceanic*, *Hauraki*, *Coastal*) is reported (right). Horizontal dashed-line boxes indicate shared haplotypes between populations.