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Worldwide Phylogeography of the genus *Delphinus* revisited

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ABSTRACT

The genus *Delphinus* comprises two species and one subspecies: the short-beaked common dolphin, *Delphinus delphis* (Linnaeus, 1758), distributed in continental shelf and pelagic waters of the Atlantic and Pacific Oceans, the long-beaked common dolphin, *D. capensis* (Gray, 1828), distributed in nearshore tropical and temperate waters of the Pacific and Southern Atlantic Oceans, and the Arabian long-beaked common dolphin, *D. capensis tropicalis* van Bree, 1971, which occurs in the Indian Ocean. Here we present a worldwide phylogeographic study based on sequences of the mitochondrial DNA cytochrome *b* gene. A total of 279 individuals were analysed: 211 *D. delphis* from the Northeast (82) and Northwest (27) Atlantic, and Northeast (28) and Southwest (74) Pacific; 26 *D. capensis* from the Northeast Pacific, 18 *D. capensis* from the Southeast Atlantic, and 24 *D. capensis tropicalis* from the Indian Ocean. Haplotype and nucleotide diversities of most populations were high when compared with other cetacean species, which is possibly a signature of large, long-term effective population size. Shared haplotypes between the two common dolphin species and subspecies were found, as well as between all oceans sampled. Fixation indices (ϕ_{ST} and F_{ST}) show that the *tropicalis* and *D. capensis* samples from the NE Pacific are differentiated from samples from all other regions. *D. delphis* from the Northeast and Southwest Pacific also show some differentiation from samples from other regions, but with relatively low values of fixation indices. In contrast, the median-joining network reveals clusters of haplotypes without a clear geographical or taxonomic correspondence. Overall, these results suggest that relatively high levels of gene flow occur between regions and possibly among recognized species, questioning current taxonomy, confounding population history and making the establishment of population boundaries very difficult. Several phylogeographical hypotheses for the observed patterns are currently being tested with recently developed methods that use coalescent models for estimating demographic parameters. Additionally, data on a powerful set of microsatellite markers are being obtained in order to document the direction and magnitude of events of recent gene flow between populations and oceanic regions.

KEYWORDS: common dolphins; short-beaked; long-beaked; Atlantic Ocean; Pacific Ocean; Indian Ocean; taxonomy; gene flow

INTRODUCTION

Common dolphins of the genus *Delphinus* are widely distributed small cetaceans that present great morphological variability throughout their distribution. At least 30 nominal species were described in the past (Hershkovitz 1966), but most cetacean biologists considered the existence of a single species (*Delphinus delphis,* Linnaeus 1758), until Heyning and Perrin (1994) found evidence for two species of common dolphins occurring in sympatry in the Northeast Pacific: the short-beaked common dolphin and the long-beaked common dolphin (*D. delphis* and *D. capensis*, respectively). These authors found differences in morphological and skeletal characters such as coloration, overall body size, length of the rostrum and tooth counts (Heyning and Perrin, 1994) and suggested that many of these differences could be assumed for other oceans. A genetic study based on the mitochondrial DNA control region gave support for the separation of the two species in that region (Rosel et al., 1994). The possible existence of a third nominal species in the Indian Ocean, *D. tropicalis* (van Bree, 1971), remained controversial until a study by Jefferson and Van Waerebeek (2002) suggested that this form is more likely a long-beaked subspecies of *D. capensis*.

Despite the new classification in two species and one subspecies, morphological studies of common dolphins inhabiting regions such as the North Atlantic and Southwest Pacific regions have shown populations with measures of rostrum length and tooth counts not matching those of the short- and long-beaked forms described for the Northeast Pacific (Bell et al., 2002; Murphy et al., 2006; Westgate, 2007). Furthermore, subsequent molecular studies using nuclear and mitochondrial DNA markers have failed to support reciprocal monophyly between the two *Delphinus* species (Amaral et al., 2007; Kingston and Rosel, 2004; LeDuc et al., 1999). In a broader study, which included samples from the North Atlantic, Mauritania, Argentina, South Africa and Northeast Pacific, including two morphologically defined long-beaked form populations, there was significant genetic differentiation among populations inhabiting different oceans, and different sides of the same ocean, but little or no differentiation among populations inhabiting the same side of an ocean basin (Natoli et al., 2006). Additionally, the authors found high differentiation among the populations described as long-beaked instead of the expected monophyly (Natoli et al., 2006). That study, however, failed to include individuals from the Indo-Pacific region; the *–tropicalis* form.

Here we revisit the worldwide phylogeography of common dolphins by conducting a combined analysis of common dolphins from the Pacific, Atlantic and Indian Oceans, including populations described as short-beaked, long-beaked and the *tropicalis* form. For this purpose we used full sequences of the mitochondrial DNA (mtDNA) cytochrome *b* gene.

MATERIAL AND METHODS

In total, 279 common dolphin samples were analysed in this study. For *D. delphis,* the sampled regions were the Northeast (NE) Atlantic, $n = 82$ (which included the Scottish coast, $n = 10$, the Irish coast, $n = 13$, the Northern Spanish coast, $n = 14$ and the West and South Portuguese coasts, $n = 45$), the Northwest (NW) Atlantic, $n = 27$, the Northeast Pacific, $n = 28$ and the Southwest (SW) Pacific, $n = 74$ (which included the Eastern Australian coast, $n = 35$, the South Australian coast, $n = 27$ and Tasmania, $n = 12$). For *D. capensis*, the sampled regions were the Northeast Pacific, $n = 26$ and the Southeast (SE) Atlantic, off South Africa, $n = 18$. These samples are here classified as *D. capensis* following Samaai et al. (2005) and P. Best (pers. comm.). Finally, for the *tropicalis*-form, $n = 21$ were obtained from the Arabian Sea in the Western Indian Ocean and $n = 3$ were obtained from the Central Indian Ocean, off the Mauritius. These later samples were only included in the haplotype network (see below).

All samples were preserved in pure ethanol. DNA was extracted from muscle or skin following standard protein K and two phenol-chloroform-isoamyl (24:1) extractions followed by ethanol precipitation (Rosel and Block, 1996). The cytochrome *b* gene was amplified (1121 bp) using

primers on the transfer RNA (tRNA) genes on either side of the cytochrome *b*. The L-strand primer was on tRNA glutamine (L14724, 5'-TGACTTGAARAACCAYCG TTG 3') and the H-strand primer on tRNA threonine (5'CCTTTTCCGGTTTACAAGAC 3'). The thermocycle profile for the cytochrome *b* gene consisted of an initial denaturation step at 94°C for 3 min followed by 35 cycles of 45 s at 94°C, 45 s at 48°Cand 1 min at 72°C and a final extension step for 5 min at 72°C. The PCR products were cleaned by adding 0.5U of Shrimp Alkaline Phosphatase and 5U of Exonuclease I and incubating at 37ºC for 30 min and 80ºC for 15 min. Both strands were directly sequenced (BigDye Terminator CycleSequencing; Applied Biosystems) on an ABI 3730 automated sequencer (Applied Biosystems).

All sequences obtained were aligned using the software Sequencher, version 4.2 (Gene Codes Corporation). Diversity measures (nucleotide and haplotype diversities) were calculated in DNAsp v.5.0 (Rozas *et al.*, 2003). To test for selective neutrality, Tajima's *D* (Tajima, 1989) and Fu's *Fs* (Fu, 1997) were also estimated in DNAsp. To test for population differentiation, pairwise F_{ST} (using haplotype frequencies) and ϕ_{ST} (using genetic distance) were calculated between sampled regions in Arlequin v. 3.11 (Excoffier et al. 2005). A Bayesian statistical method for the estimation of hidden genetic structure of populations was also implemented in BAPS v. 5.0 (Corander and Marttinen, 2006). A median-joining network of haplotypes was constructed in NETWORK v. (Bandelt *et al.*, 1999). A Bayesian phylogenetic tree was obtained in MrBayes v. 3.1.2. (Huelsenbeck and Ronquist, 2001) by running four simultaneous MCMC chains for 2 million generations, with trees sampled at intervals of 100 generations. The first 3000 trees were discarded as "burn-in". Sequences of *Stenella coeruleoalba* and *Tursiops truncatus* were used as outgroups.

RESULTS

The 1121 bp analysed for the cytochrome *b* gene revealed 391 polymorphic sites, defining 141 haplotypes (Appendix 1). Shared haplotypes (4) between all the three forms (*-delphis*, *-capensis* and *–tropicalis*) were found, as well as between several geographical regions sampled (Appendix 1). Haplotypic and nucleotide diversities were high for most putative populations analysed, with *D. delphis* from the NE Pacific showing the highest nucleotide and haplotypic diversities and the *tropicalis* form showing the lowest haplotypic diversity (Table 1). The neutrality tests revealed negative and highly significant values of Fu's *Fs* for NE and NW Atlantic and NE and SW Pacific, suggesting that these populations are in expansion.

Pairwise F_{ST} and ϕ_{ST} values show s significant levels of genetic differentiation between most putative populations, with ϕ_{ST} values being generally higher than F_{ST} values (Table 2). This suggests that, at a population level, the differentiation observed is not recent. The *D. capensis* population from NE Pacific is highly differentiated from all other populations, being less differentiated from the *D. delphis* population from the same region. The South African population and the *–tropicalis* population from the Indian Ocean are also highly differentiated from all other populations. The analysis of hidden population structure performed in BAPS identified four clusters in the optimal partition (log likelihood of -4421-354). These clusters are identified in the median-joining network (Figure 1) and show no obvious relationship with geographical origin of samples or with current taxonomy. This is quite surprising given the significant levels of differentiation obtained with pairwise F_{ST} and ϕ_{ST} values. However, this may be due to the low number of haplotypes shared between some geographical regions. The existence of a central, likely ancestral haplotype is not clear, although H23, found in *D. delphis* from NE and NW Atlantic and SW Pacific occupies a central position in Cluster 2. This cluster includes most *D. delphis* haplotypes from the NE and NW Atlantic and from the SW Pacific but also *D. capensis* from the SE Atlantic and *D. c. tropicalis* from the Indian Ocean. Cluster 3 is highly differentiated from all others, with the most common haplotype being found in *D. c. tropicalis* from the Indian Ocean, in *D. capensis* from NE Pacific and in *D. delphis* from the NW Atlantic (one individual from SE Atlantic is also present in this group). This cluster had already been identified in a previous study including only common dolphins from the NE Atlantic (Amaral et al. 2007).

Cluster 1 includes *D. capensis* from the NE Pacific and *D. c. tropicalis* from the Indian Ocean, and in the phylogenetic tree derives from haplotypes found in the NE and SW Pacific. Finally, cluster 4 includes only haplotypes found in *D. delphis* from the NE and SW Pacific.

In the Bayesian phylogenetic tree obtained, only Clusters 1 and 3 are monophyletic (Figure 2). Cluster 3 occupies a basal position in the tree, supported by a high posterior probability value, and is probably the oldest (Figure 2). Cluster 1, which contains most of *D. capensis* from the NE Pacific derives from *D. delphis* haplotypes from the NE and SE Pacific (Figure 2).

DISCUSSION

The results of this study show that the distribution and sorting of maternal lineages in common dolphins (inferred based on cytochrome *b* sequences) does not agree with the current taxonomy of the genus *Delphinus*. Both the median-joining network and the Bayesian phylogenetic tree show that *Delphinus delphis*, *D. capensis* and *D. c. tropicalis* are not monophyletic. This result is not new (Amaral et al. 2007; LeDuc et al. 1999) and can be due to several factors including incomplete lineage sorting, hybridization and incorrect taxonomy. The shape of the network and the short branch lengths seen in the Bayesian phylogenetic tree suggest that the genus originated through a rapid radiation. In this case, ancestral allelic lineages may not have yet completely sorted leading to the retention of ancestral polymorphisms (Hudson, 1992).

The presence of shared haplotypes between the two common dolphin species and subspecies can also be indicative of hybridization. When species are recently separated, great part of the genome have probably not accumulated enough fixed differences to prevent hybridization in cases of secondary contact (Wu, 2001).

Finally, current taxonomy may be incorrect. The large morphological variability seen in common dolphins throughout their distribution, particularly differences related to the length of the rostrum, tooth counts and coloration seem to be plastic, therefore influenced by the environment, and may represent local adaptations. Hence, identifying species or even stocks based on morphology alone can be misleading because the evolutionary potential of a stock, subspecies or species is harboured in their genetic similarities and not in their external appearance. This seems to be the case of common dolphins, where morphological similarities do not agree with genetic similarities. For example, common dolphins from South Africa have been described as belonging to the long-beaked form but a recent morphological study identified some individuals falling outside the range of the short-beaked form (Samaai et al., 2005). One of the specimens used in the study by Samaai et al. (2005), which was classified according to coloration criteria as having 85.7% characteristics of the long-beaked form and 14.3% characteristics of the short-beaked form, shares a haplotype with short-beaked specimens from the North Atlantic and SW Pacific (Haplotype 29 in the network). Moreover, this population from South Africa is highly differentiated from the long-beaked population from the NE Pacific, as also found by Natoli et al. (2006), suggesting that the long-beaked morphology is a result of local adaptation.

Long-beaked common dolphin populations have been described to occur in a few nearshore continental shelf areas in the Pacific (e.g. Baja California, Mexico, off Peru, Southern Japan, Korea and Southern China) and Atlantic (e.g. off Venezuela and Southern Brazil) Oceans, with the *tropicalis* form being restricted along continental margins of the Indian Ocean (Amaha, 1994; Heyning and Perrin, 1994; Jefferson et al., 2009; Jefferson and Van Waerebeek, 2002). However, the question of whether these groups of common dolphins are indeed separate species or not remain unanswered. The fact that the long-beaked population inhabiting the NE Pacific is differentiated from the short-beaked population from the same region suggests a case of local adaptation and incipient speciation.

If reciprocal monophyly of maternal lineages is used to delineate species of *Delphinus* (see De Queiroz, 2007 for a distinction between species delimitation and species conceptualization), then

our study suggests that common dolphins represent a single and widely distributed 'super species'. The four main clusters obtained do not agree with taxonomy (i.e., designation into short-beaked and long-beaked populations) or with the geographical origin of individuals. Nonetheless, we identified a number of partially isolated populations, including here groups of lineages that likely display a high degree of local adaptation and are perhaps in the process of incipient speciation. Our preliminary results based on microsatellite DNA data (Amaral et al., unpublished) also seem to support the distinction of these several partially isolated populations. Thus, the existence of different stocks of common dolphins in the different oceans is supported by this study and this should be taken into consideration when designing and implementing management strategies.

In summary, our study illustrates the difficulties in delineating taxonomic units in *Delphinus* using a molecular genealogical perspective. The distribution of the different morphotypes in the different geographic regions is not seen in the distribution of mitochondrial lineages, which puts into question current morphology-based taxonomy. Further analysis including geographic regions not sampled in this study, additional molecular markers and more powerful statistical analyses are currently under way to (i) clarify patterns of population history, their chronology and temporal progression, (ii) test for historical and contemporary hybridization between taxa, and (iii) assess levels of gene flow between major oceanic regions.

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Table 1. Genetic diversity measures and neutrality tests for the geographical regions sampled of short-beaked common dolphins (*Delphinus delphis*), long-beaked common dolphin (*D. capensis*) and the Arabian common dolphins (*D. c. tropicalis*).

Species	**Region**	***n***	**π**	***h***	***D***	***Fs***
Delphinus delphis	Irish coast	14	0.00827	0.956	0.22820	-1.64675
	Scotish coast	10	0.00339	0.911	-0.47046	-1.41717
	Northern Spain	13	0.00748	0.949	-0.58200	-1.35048
	Portuguese coast	45	0.00452	0.913	-1.54043	**-6.66568**
	NE Atlantic	82	0.00565	0.925	-1.19835	**-11.70000**
	SW Pacific (NSW)	35	0.00598	0.931	-1.74705	**-7.73805**
	SW Pacific (SA)	27	0.00539	0.972	-1.09738	**-7.75900**
	SW Pacific (TAS)	12	0.00724	0.985	-0.82100	**-3.55676**
	SW Pacific	74	0.00609	0.975	**-1.87112**	**-33.05300**
	NW Atlantic	27	0.00602	0.969	-0.15570	**-6.87500**
	NE Pacific	28	0.01019	0.992	-1.75949	**-11.77300**
D. capensis	NE Pacific	26	0.00445	0.858	0.17571	0.71200
	South Africa coast	18	0.00498	0.824	-1.57091	-0.69100
D. c. tropicalis	W Indian	21	0.00500	0.548	-0.47729	**4.72900**
Mean		278	0.00488	0.954	**-2.32133**	**-124.97500**

n – number of individuals sequenced; π - nucleotide diversity; *h* – haplotypic diversity; *D* – Tajima's *D*; *Fs* – Fu's *Fs*.

Table 2. Pairwise F_{ST} (below diagonal) and ϕ_{ST} (above diagonal) values for the different geographical regions sampled.

	Dd NEATL	Dd NWATL	Dc SAFR	Dd SWPAC (NSW)	Dd SWPAC (SA)	Dd SWPAC (TAS)	Dd NEPAC	Dct WIND	Dc NEPAC
Dd_NEATL		0.11034**	0.05486*	0.13153***	0.04255*	0.06610*	0.16514***	0.52880***	0.50974***
Dd_NWATL	0.03399**		0.16591**	0.18320***	0.15520***	0.10538*	0.11091**	0.28812***	0.43754***
Dc_SAFR	0.08595***	0.06669***		0.14048***	0.04046*	0.08570*	0.20519***	0.59535***	0.54237***
Dd_SWPAC (NSW)	0.07224***	0.04618***	0.10108***		0.04038*	0.02685	0.09453***	0.55103***	0.48317***
Dd_SWPAC (SA)	0.04516***	0.01339	0.06816***	0.04251***		0.01421	0.12066***	0.57561***	0.49199***
Dd_SWPAC (TAS)	0.04838**	0.01918*	0.07885**	0.02288	0.01459		0.03261	0.51888***	0.44278***
Dd_NEPAC	0.04346***	0.01567**	0.07081***	0.03913***	0.01709**	0.01168		0.40357***	0.37258***
Dt_WIND	0.23042***	0.16696***	0.29706***	0.24353***	0.22858***	0.25324***	0.21993***		0.57837***
Dc_NEPAC	0.08748***	0.05398***	0.11872***	0.08486***	0.06349***	0.06124**	0.05493***	0.225***	

*P<0.05; **P<0.01, ***P<0.001

NEATL – Northeast Atlantic; NWATL – Northwest Atlantic; SWPAC – Southwest Pacific; NEPAC – Northeast Pacific; WIND – Western Indian Ocean; SWATL – Southwest Atlantic. Dd – *Delphinus delphis*; Dc – *D. capensis*; Dt – *D. c. tropicalis*.

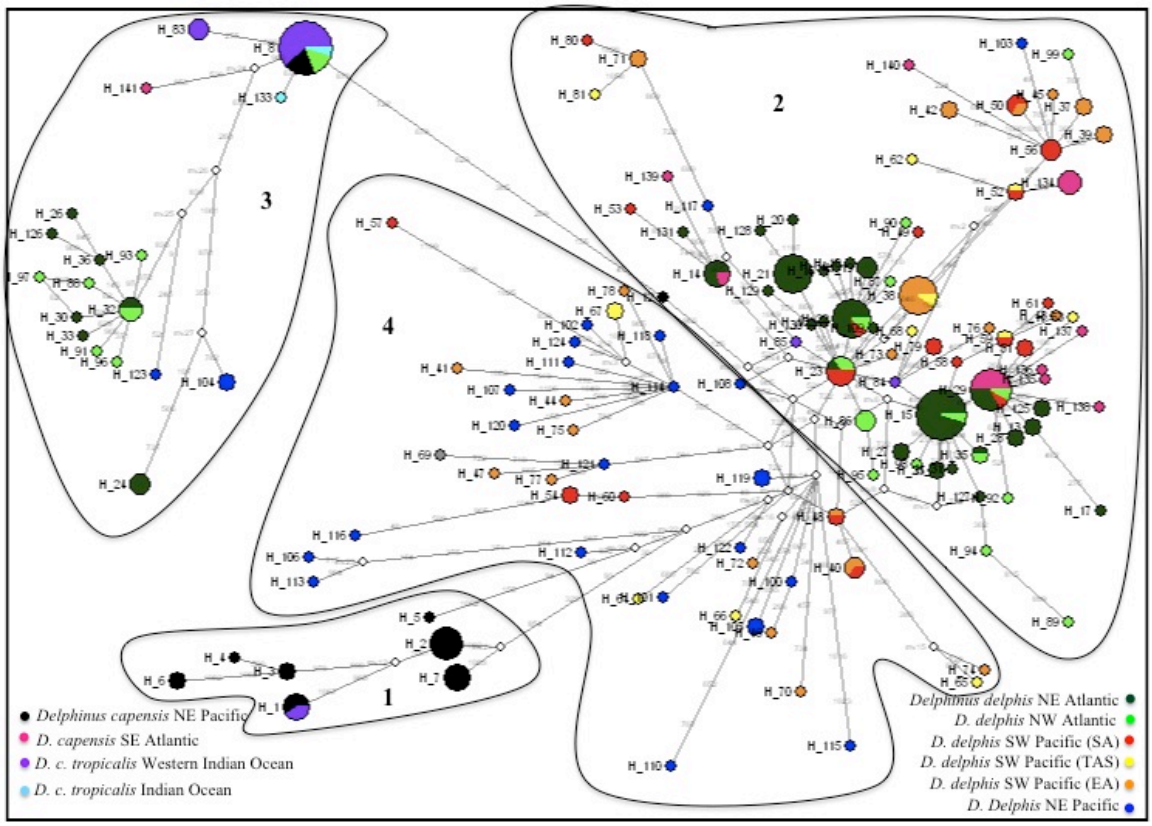

Figure 1. Median-joining network of common dolphin cytochrome *b* gene haplotypes. Circle size is proportional to the number of individuals exhibiting the corresponding haplotype and proportional of each population within each haplotype is coloured according to the legend. Length of lines is proportional to the number of mutational steps separating haplotypes. White circles indicate missing intermediate haplotypes.

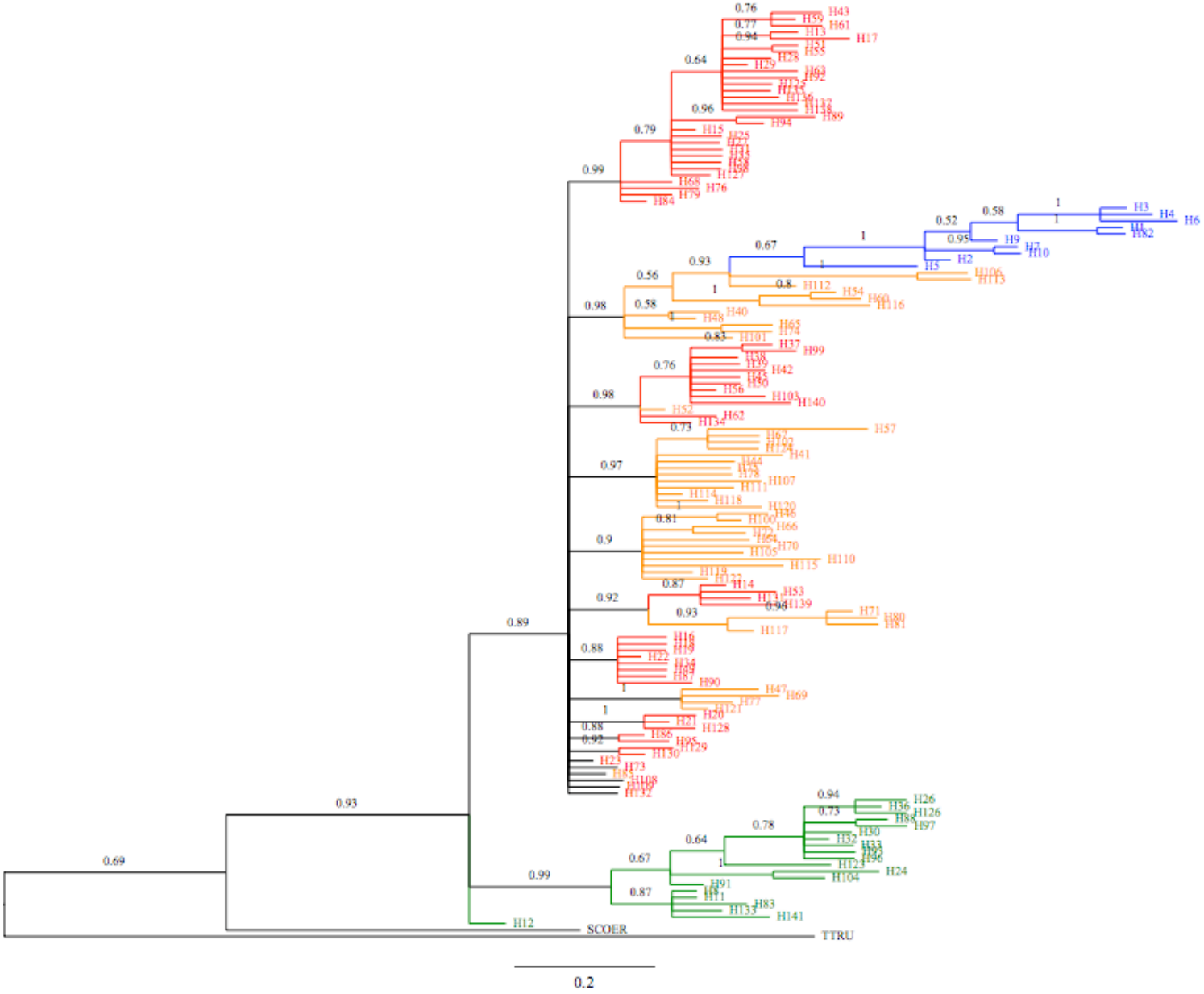

Figure 2. Bayesian phylogenetic tree of common dolphin cytochrome *b* haplotypes. Posterior probability values are above branches. Colours designate the clusters obtained by BAPS and showned in the network. Blue corresponds to Cluster 1, red to cluster 2, green to cluster 3 and orange to cluster 4.

Appendix 1. Haplotype list.

Haplotype	Frequency									
	Dd NEATL	NWATL	SWPAC (NSW)	SWPAC (SA)	SWPAC (TAS)	NEPAC	Dt WIND	Dc NEPAC	SAFR	Total
1							1	3		4
2								7		7
3								2		2
4								1		1
5								1		1
6								2		2
7								4		4
8		3					15	2		20
9								1		1
10								1		1
11								1		1
12								1		1
13	2									2
14	4								1	4
15	18	1								19
16	1									1
17	1									1
18	1									1
19	3									3
20	1									1
21	10									10
22	8	1		1						10
23	1	2		3						6
24	3									3
25	2									2
26	1									1
27	2									2
28	2									2
29	4	1		1					6	6
30	1									1
31	1									1
32	2	2								4
33	1									1
34	1									1
35	1	1								2
36	1									1
37			2							2
38			9		1					10
39			2							2
40			2	1						3
41			1							1
42			2							2
43			1							1
44			1							1
45			1							1
46			1							1
47			1							1
48			1	1						2

Appendix 1. (*cont.*)

Haplotype	Frequency									
	Dd		SWPAC	SWPAC	SWPAC		Dt	Dc		
	NEATL	NWATL	(NSW)	(SA)	(TAS)	NEPAC	WIND	NEPAC	SAFR	Total
49				1						1
50			1	2						3
51				1						1
52				1	1					2
53				1						1
54				2						2
55				1						1
56				3						3
57				1						1
58				1						1
59				1	1					2
60				1						1
61				1						1
62					1					1
63					1					1
64					1					1
65					1					1
66					1					1
67					2					2
68					1					1
69			1							1
70			1							1
71			2							2
72			1							1
73			1							1
74			1							1
75			1							1
76			1							1
77			1							1
78			1							1
79				2						2
80				1						1
81					1					1
82							1			1
83							3			3
84							2			2
85							2			2
86		3								3
87		1								1
88		1								1
89		1								1
90		1								1
91		1								1
92		1								1
93		1								1
94		1								1
95		1								1
96		1								1

Appendix 1. (*cont.*)

Haplotype	Frequency									
	Dd		SWPAC	SWPAC	SWPAC		Dt	Dc		
	NEATL	NWATL	(NSW)	(SA)	(TAS)	NEPAC	WIND	NEPAC	SWATL	Total
97		1								1
98		1								1
99		1								1
100						1				1
101						1				1
102						1				1
103						1				1
104						2				2
105						2				2
106						1				1
107						1				1
108						1				1
109	1									1
110						1				1
111						1				1
112						1				1
113						1				1
114						1				1
115						1				1
116						1				1
117						1				1
118						1				1
119						2				2
120						1				1
121						1				1
122						1				1
123						1				1
124						1				1
125	2									2
126	1									1
127	1									1
128	1									1
129	1									1
130	1									1
131	1									1
132	1									1
133							1			1
134									4	0
135									1	0
136									1	0
137									1	0
138									1	0
139									1	0
140									1	0
141									1	0

NEATL – Northeast Atlantic; NWATL – Northwest Atlantic; SWPAC – Southwest Pacific; NEPAC – Northeast Pacific; WIND – Western Indian Ocean; SWATL – Southwest Atlantic. Dd – *Delphinus delphis*; Dc – *D. capensis*; Dt – *D. c. tropicalis*.