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COASTAL BOTTLENOSE DOLPHINS FROM SOUTHEASTERN AUSTRALIA ARE *TURSIOPS ADUNCUS* ACCORDING TO SEQUENCES OF THE MITOCHONDRIAL DNA CONTROL REGION

LUCIANA M. MÖLLER
Graduate School of the Environment,
Macquarie University, NSW, 2109, Australia
E-mail: lmoller@ecosys.gse.mq.edu.au

LUCIANO B. BEHEREGARAY
Department of Biological Sciences,
Macquarie University, NSW, 2109, Australia

ABSTRACT

Sequence analysis of the mitochondrial DNA control region was used to clarify the taxonomic status of two coastal bottlenose dolphin populations from southeastern Australia currently classified as *Tursiops truncatus*. A 368-bp segment of the control region of 57 biopsy-sampled, photo-identified dolphins of Jervis Bay and Port Stephens was compared to published sequences of *T. truncatus* and *T. aduncus* from different oceanic regions. Sequence divergence between haplotypes from southeastern Australia and *T. aduncus* was much lower than that from *T. truncatus*. Analyses using two different methods of phylogenetic reconstruction unambiguously placed all haplotypes from southeastern Australia in a group composed exclusively of *T. aduncus*. The results strongly indicated that these two bottlenose dolphin populations belong to *T. aduncus*, extending the range of the species to subtropical waters of the Western South Pacific Ocean.

Key words: bottlenose dolphin, *Tursiops aduncus*, *Tursiops truncatus*, mitochondrial DNA control region, taxonomy, phylogenetic analysis, southeastern Australia.

Bottlenose dolphins (genus *Tursiops*) are cosmopolitan in tropical and temperate waters, and include both coastal and pelagic populations (Rice 1998). Due to their wide distribution and variation in morphological characters, many species and subspecies were initially described, the consequences of which was a long period of taxonomic confusion. Currently *T. truncatus* (Montagu, 1821), originally described for the North Atlantic Ocean, is considered a widespread

species comprised of both nearshore and offshore forms (*e.g.,* Ross and Cockcroft 1990, Mead and Potter 1995, Curry and Smith 1997, Hoelzel *et al.* 1998). Other species, such as *T. gillii* (Dall, 1873) and *T. nuuanu* from the Eastern Pacific Ocean, and *T. gephyreus* (Lahille, 1908) from the Western South Atlantic, are today considered synonyms of *T. truncatus* (Rice 1998). The only other congeneric species presently recognized is *T. aduncus* (Ehrenberg, 1832). It is distributed in coastal waters of the Indo-Pacific and Indian Ocean, including northern Australia (Rice 1998). South African bottlenose dolphins were previously classified as either *T. aduncus* or *T. truncatus* on the basis of differences in size and morphological characters (Ross 1977). However, Ross and Cockcroft (1990) recommended that South African and Australian bottlenose dolphins be assigned to *T. truncatus* after latitudinal variation was found in Australian bottlenose dolphins from both west and east coasts. Furthermore, the authors proposed that populations in which adult individuals were ventrally spotted should be named a subspecies of *T. truncatus.* Contemporary publications dealing with eastern Australian bottlenose dolphins have adopted *T. truncatus* as the name of dolphins in this region (*e.g.,* Corkeron 1990, 1997; Möller and Harcourt 1998).

Recently analyses of external morphology and osteology of sympatric *aduncus* and *truncatus* forms in Chinese waters showed that *T. aduncus* is a distinct species from *T. truncatus* (Wang *et al.,* 2000 *a, b*). This was supported by two independent phylogenetic studies of mitochondrial DNA (mtDNA) (LeDuc *et al.* 1999, Wang *et al.* 1999). Moreover, mtDNA control region sequences of *T. truncatus* from Chinese waters are more closely related to *T. truncatus* from the Atlantic Ocean than to the sympatric *T. aduncus* (Wang *et al.* 1999). A mtDNA cytochrome *b* analysis of delphinids revealed possible polyphyly of *Tursiops,* but the authors recommended that until a taxonomic revision of the subfamily Delphininae clarifies generic names, *T. aduncus* should be accepted as a valid species (LeDuc *et al.* 1999). These studies identify considerable uncertainty regarding the taxonomic status of Australian bottlenose dolphins. Furthermore, the boundaries of the distribution of *T. aduncus,* including its presence or absence in areas of the Pacific Ocean, remain unknown.

Since 1997 we have been studying two coastal populations of southeastern Australian bottlenose dolphins inhabiting Jervis Bay (JB) and Port Stephens (PS) (Fig. 1). These populations have been the focus of regular photo-identification, behavioral observations, and biopsy sampling as part of an ongoing study of their social structure and genetic relationships.

The highly variable control region of the mtDNA has been used in a variety of cetacean species to investigate population structure (*e.g.,* humpback whales, Baker *et al.* 1998; Hector's dolphins, Pichler *et al.* 1998), interspecific phylogenetic relationships (*e.g.,* common dolphins, Rosel *et al.* 1994; bottlenose dolphins, Wang *et al.* 1999), and for genetic identification of specimens (beaked whales, Dalebout *et al.* 1998; whale and dolphin products, Baker *et al.* 1996). In this paper we analyze the mtDNA control region of bottlenose dolphins from JB and PS, and compare them to published sequences of *T.*

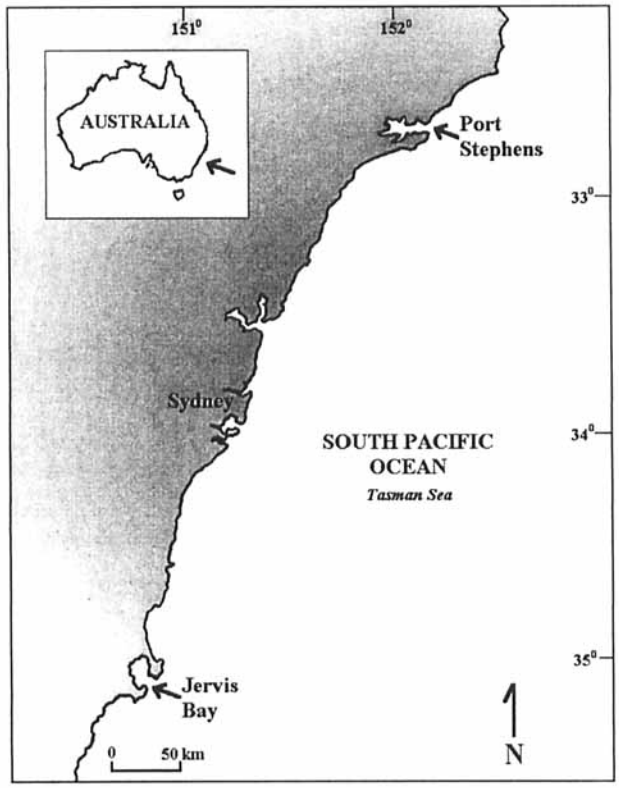

Figure 1. Location of Jervis Bay and Port Stephens in southeastern Australia.

truncatus and *T. aduncus,* to clarify the taxonomic status of our study populations.

Materials and Methods

Biopsy samples composed of skin and blubber were collected from bottlenose dolphins from a distance of about 10 m using a rifle modified to deliver biopsy darts (Biopsy equipment .745 series, PAXARMS[1]) with cutting heads 6 mm wide and 8 mm long. Samples were preserved in 20% dimethyl sulphoxide (DMSO) saturated with sodium chloride (Amos and Hoelzel 1991). Dolphins were photographed at time of sampling for photo-identification (Würsig and Jefferson 1990). Only samples taken from positively identified individuals (JB, $n = 17$; PS, $n = 40$) were used for analyses. No samples from dependent calves were included. Based on photo-identification studies, all these individuals are known to have high site fidelity to the area where they were sampled, with the exception of two dolphins which are considered occasional visitors to JB (Möller and Harcourt 1998; L. Möller, unpublished data).

[1] PAXARMS N.Z. LTD. 37 Kowhai Street, Timaru, New Zealand.

Table 1. Sequences of mtDNA control region of *T. aduncus* (Tadu) and *T. truncatus* (Ttru) from different localities used for comparison with bottlenose dolphin haplotypes from southeastern Australia (SEAust). *L. acutus* (Lacu) was outgroup used for phylogenetic analyses.

Haplotype	GenBank accession number	Locality	Reference
Tadu1	AF056233	China and Taiwan, Indo-Pacific	Wang *et al.* (1999)
Tadu2	AF056234	China, Indo-Pacific	Wang *et al.* (1999)
Tadu3	AF056235	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Tadu4	AF056236	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Tadu5	AF056237	Indonesia, Indo-Pacific	Wang *et al.* (1999)
Tadu6	AF056238	Indonesia, Indo-Pacific	Wang *et al.* (1999)
Tadu7	AF056239	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Tadu8	AF056240	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Tadu19	AF056241	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Tadu10	AF056242	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Tadu11	AF056243	Taiwan, Indo-Pacific	Wang *et al.* (1999)
SEAust1	AF287951	Australia, SW Pacific	this study
SEAust2	AF287952	Australia, SW Pacific	this study
SEAust3	AF287953	Australia, SW Pacific	this study
SEAust4	AF287954	Australia, SW Pacific	this study
SEAust5	AF287955	Australia, SW Pacific	this study
Ttru1	AF056219	Brazil, SW Atlantic	Wang *et al.* (1999)
Ttru2	AF056220	Hong Kong and Taiwan, Indo-Pacific	Wang *et al.* (1999)
Ttru3	AF056221	Hong Kong, Indo-Pacific	Wang *et al.* (1999)
Ttru4	AF056222	Mauritania, NE Atlantic	Wang *et al.* (1999)
Ttru5	AF056223	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Ttru6	AF056224	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Ttru7	AF056225	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Ttru8	AF056226	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Ttru9	AF056227	Taiwan, Indo-Pacific	Wang *et al.* (1999)

Table 1. Continued.

Haplo-type	GenBank accession number	Locality	Reference
Ttru10	AF056228	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Ttru11	AF056229	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Ttru12	AF056230	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Ttru13	AF056231	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Ttru14	AF056232	Taiwan, Indo-Pacific	Wang *et al.* (1999)
Ttru15	U20910	USA, NW Atlantic	Siemann (1994)
Ttru16	U20911	USA, NW Atlantic	Siemann (1994)
Ttru17	U20912	USA, NW Atlantic	Siemann (1994)
Ttru18	U20913	USA, NW Atlantic	Siemann (1994)
Ttru19	U20914	USA, NW Atlantic	Siemann (1994)
Ttru20	U20915	USA, NW Atlantic	Siemann (1994)
Ttru21	U20916	USA, NW Atlantic	Siemann (1994)
Ttru22	U20917	USA, NW Atlantic	Siemann (1994)
Ttru23	U20919	USA, NW Atlantic	Siemann (1994)
Ttru24	U20920	USA, NW Atlantic	Siemann (1994)
Lacu	AF113487	NW Atlantic	Cipriano (1997)

Genomic DNA was extracted by proteinase K digestion followed by DNA isolation with a salting-out method (Sunnucks and Hales 1996). A fragment of approximately 460-bp of the mtDNA control region was amplified by the polymerase chain reaction (PCR) with primers Dlp-1.5 (5′-TCA-CCCAAAGCTGRARTTCTA-3′) and Dlp-5 (5′-CCATCGWGATGTCT-TATTTAAGRGGAA-3′) from Baker *et al.* (1993). PCR conditions consisted of an initial denaturation at 93°C/3 min, followed by a nine-cycle touch-down (93°C/30 sec, annealing at 63°C down 1 degree per cycle until 55°C, and 72°C/1 min). The next cycle was repeated 27 times at an annealing of 53°C/30 sec, with final extension at 72°C/5 min. Amplified fragments were screened for sequence variation by the single-stranded conformation polymorphism (SSCP) analysis as described in Sunnucks *et al.* (2000). SSCP is a convenient and economical technique for identifying fragments with the same or different DNA sequence (Orita *et al.* 1989, Sunnucks *et al.*, 2000). Representatives of identified SSCP phenotypes were sequenced in an ABI 377 DNA sequencing system according to manufacturer's instructions. The reliability of the technique was tested by comparing the DNA sequences of different individuals with the same SSCP phenotype (see Results).

Haplotype sequences were reduced in length to allow alignment with sequences of 25 *T. truncatus,* 11 *T. aduncus,* and one *Lagenorhynchus acutus* available in GenBank (Table 1). Sequence divergence was calculated among haplotypes and their phylogenetic relationships inferred by maximum parsimony (MP) and neighbor-joining distance (NJ) methods using PAUP* (Swofford 1998). MP trees were obtained using both unweighted and weighted (transversions nine times over transitions) character analysis. The NJ tree was estimated using the Kimura 2-parameter genetic distance model (Kimura 1980) with a gamma distribution (shape parameter = 0.5). Reliability of tree nodes for MP and NJ phylogenies was assessed using 1,000 bootstrap replicates. The *L. acutus* sequence was used as the outgroup for phylogenetic analyses.

Results

Five control region phenotypes were distinguished by SSCP analysis among the 57 coastal bottlenose dolphins from the two southeastern Australian populations. The number of individuals sharing a unique SSCP phenotype and the number of replicates sequenced per phenotype were as follows: 23 of phenotype 1 (8 sequenced), 30 of phenotype 2 (10 sequenced), one of phenotype 3 (one sequenced), one of phenotype 4 (one sequenced), and two of phenotype 5 (two sequenced). Sequence analysis of 403-bp from the 22 individuals con-

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Table 2. Polymorphic sites from 368-bp of mtDNA control region of bottlenose dolphins from southeastern Australia in comparison to GenBank sequences of *T. aduncus* and *T. truncatus*, and one *L. acutus*. Positions that did not vary in relation to top haplotype omitted, and hyphen denotes deletion.

Nucleotide position

Haplotype	1	9	12	13	26	31	33	36	37	43	44	45	50	52	55	60	64	66	73	77	78	79	83	84	85	97	98	100	101	103	104	113	115	117	118	136	139	162	172	173	181	186	202	210	213	216	230	232	233	237	240	241	242	244	245	246	247	248	250	251	252	262	271	273	278	282	284	293	325	338	359	360	361
Tadu1	T	C	T	G	G	T	G	T	T	C	A	T	C	G	C	C	T	C	A	G	T	A	G	C	T	T	C	C	C	T	G	C	T	T	A	T	G	T	T	C	T	T	T	A	C	G	T	T	G	C	T	T	A	T	T	T	-	C	C	C	C	C	G	T	T	T	A	A	T	C	C	C	C
Tadu2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	A	C	.	.	.	.	.	T	.	.	T
Tadu3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	A	C	.	.	.	.	.	T	.	.	T
Tadu4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.
Tadu5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	A	.	.	.	.	.	.	.	.	.	.	.	.	C	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	C	.	.	.	.	.	T	.	.	T
Tadu6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	T	.	A	C	.	.	.	.	.	T	.	.	T
Tadu7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	A	C	.	.	.	.	.	T	.	T	T
Tadu8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	C	.	.	C	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	A	.	.	.	.	.	.	T	.	.	T
Tadu9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	T	.	.	.
Tadu10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	C	.	.	.	.	.	T	.	.	T
Tadu11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	A	C	.	.	.	.	.	T	.	T	T
SEAust1	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	T	.	.	T
SEAust2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	C	.	.	.	.	.	T	.	.	T
SEAust3	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	C	.	.	.	.	.	T	.	.	T
SEAust4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	T	.	.	T
Ttru1	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	C	.	A	C	.	.	.	.	.	.	A	.	A	.	C	A	.	.	C	T	.	.	T	.	.	.	.	.	.	.	.	.	.	.	T
Ttru2	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	T	A	C	.	.	T	.	.	.	C	.	A	.	C	A	.	C	C	T	.	.	T	.	A	.	.	.	.	.	C	T	.	.	T
Ttru3	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	.	G	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	A	C	.	.	T	.	.	C	C	.	A	.	C	A	C	C	T	T	T	.	T	.	A	.	.	.	.	.	C	T	.	T	T
Ttru4	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	C	T	A	C	.	.	.	.	.	.	A	.	A	.	C	A	.	.	C	T	.	.	T	.	.	.	.	.	.	.	.	.	T	A	T
Ttru5	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	C	.	A	C	.	.	T	A	.	.	C	.	A	.	C	A	.	C	C	T	.	.	T	.	A	.	C	.	.	.	C	T	T	.	T
Ttru6	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	T	A	C	.	.	.	.	.	.	C	.	A	.	C	A	.	C	C	T	.	T	T	.	A	.	.	.	.	.	C	T	T	.	T
Ttru7	C	G	.	.	.	C	.	.	.	.	.	.	.	.	.	T	.	T	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	A	C	.	.	.	.	.	.	C	.	A	.	C	A	.	C	C	T	.	T	T	.	A	.	.	.	.	.	C	T	T	.	T
Ttru8	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	C	.	A	C	.	.	T	.	.	.	C	.	A	.	C	A	.	C	C	T	.	.	T	.	A	.	C	C	.	.	C	T	T	.	T
Ttru9	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	A	C	.	.	.	.	.	.	C	.	A	.	C	A	.	C	C	T	.	T	T	.	A	.	.	.	.	.	C	T	T	.	T
Ttru10	C	G	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	A	C	.	.	T	A	.	.	C	.	A	.	C	A	.	C	C	T	T	.	T	.	A	.	.	.	.	.	C	T	T	.	T
Ttru11	.	G	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	.	G	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	A	C	.	.	T	.	.	C	C	.	A	.	C	A	C	C	T	T	T	.	T	.	A	.	.	.	.	.	C	T	.	T	T
Ttru12	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	T	A	C	.	.	T	.	.	.	C	.	A	.	C	A	.	.	C	T	.	.	T	.	A	.	.	.	.	.	C	T	.	.	T
Ttru13	C	G	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	T	A	C	.	.	T	.	.	.	C	.	A	.	C	A	.	C	C	T	.	.	T	.	A	.	.	.	.	.	C	T	.	.	T
Ttru14	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	T	A	C	.	.	.	.	.	.	T	.	A	.	C	A	.	.	T	.	T	T	T	.	A	.	.	.	.	G	C	T	.	.	.
Ttru15	C	.	C	T	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	A	C	.	.	.	.	.	.	C	T	A	.	C	A	.	C	C	T	.	.	T	.	A	.	.	.	.	.	C	T	T	.	T
Ttru16	.	.	C	T	.	.	.	.	.	.	.	.	.	.	.	T	.	T	G	.	.	G	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	C	.	A	C	C	.	T	.	.	.	A	.	A	.	-	A	.	C	T	T	.	.	T	.	.	.	.	.	G	.	.	T	.	.	T
Ttru17	.	.	C	C	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	C	C	.	A	C	.	.	T	.	.	.	A	T	A	.	C	A	.	C	T	T	T	.	T	T	.	.	.	.	.	.	.	T	.	.	T
Ttru18	.	.	C	T	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	C	T	A	C	.	.	T	.	.	.	A	.	A	.	C	A	.	C	T	T	.	.	T	T	.	.	.	.	.	.	.	T	.	.	T
Ttru19	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	C	.	A	C	.	.	.	.	.	.	A	.	A	.	C	A	.	C	C	T	T	.	T	T	.	.	.	.	.	.	C	T	.	.	T
Ttru20	C	.	C	T	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	C	C	.	A	C	.	.	T	.	.	.	A	.	A	.	C	A	.	C	T	T	.	.	T	.	.	.	.	.	.	.	C	T	.	.	T
Ttru21	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	A	C	.	.	.	.	.	.	C	.	A	.	C	A	.	C	C	T	.	.	T	.	A	.	.	.	.	.	C	T	.	.	T
Ttru22	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	C	C	.	A	C	.	.	T	.	.	.	C	.	A	.	C	A	.	C	T	T	.	.	T	.	.	.	.	.	.	.	.	T	.	.	T
Ttru23	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	T	A	C	.	.	T	.	.	.	A	T	A	.	C	A	.	C	C	T	T	.	T	.	A	.	.	.	.	.	C	T	.	.	T
Ttru24	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	T	A	C	.	.	T	.	.	.	C	T	A	.	C	A	.	C	C	T	T	.	T	.	A	.	.	.	.	.	C	T	.	.	T
L. acutus	C	.	.	.	A	.	.	C	C	A	C	A	T	A	T	.	C	.	.	A	.	.	.	T	C	C	T	T	T	C	A	T	.	.	G	.	.	.	C	.	A	C	.	T	.	.	C	.	A	.	A	A	C	A	.	.	T	T	T	T	T	.	.	.	.	.	.	.	.	T	.	-	T

firmed that different SSCP phenotypes had different sequences, and that dolphins with the same phenotype had identical sequences. Thus, phenotypes are hereafter called SEAust haplotypes. Haplotype SEAust1 was found in seven individuals in JB and 16 in PS, while haplotype SEAust2 was represented in 8 samples in JB and 22 in PS. Haplotypes SEAust3 and SEAust4 occurred once each in JB, and only two individuals in PS had haplotype SEAust5. Haplotypes represented by only one individual were from year-round resident dolphins, while the two sampled individuals considered occasional visitors in JB each had one of the common haplotypes. Sequences of the SEAust haplotypes were deposited in GenBank under Accession numbers AF287951-AF287955.

We unambiguously aligned SEAust sequences with 368-bp of the GenBank sequences. SEAust5 was dropped from the analysis because it was identical to SEAust1 except for one transitional difference which was outside the aligned region. None of the SEAust haplotypes matched *Tursiops* haplotypes from GenBank. Fifty variable sites were found among *Tursiops* sequences, and 73 including *L. acutus* (Table 2). For *Tursiops,* 41 of these sites were transitions, four were transversions, three exhibited both, one was an insertion/deletion or a transition, and one was an insertion/deletion or a tranversion. Eight of these sites had fixed differences between published *T. aduncus* and *T. truncatus* sequences, including one insertion/deletion event. SEAust haplotypes were identical to *T. aduncus* at all eight sites.

Sequence divergence between *T. aduncus* and *T. truncatus* ranged from 4.1% to 7.1% (15 to 26 substitutions, respectively) (Table 3). For *T. aduncus* and SEAust haplotypes it varied from 0.5% to 2.2% (2 to 8 substitutions, respectively), while between *T. truncatus* and SEAust haplotypes it ranged from 4.6% to 7.4% (17 to 27 substitutions, respectively).

Regardless of the method used to estimate phylogenies (weighted or unweighted MP, or NJ), tree topologies were identical in separating two major groups, each of which contained only *T. aduncus* or *T. truncatus.* All SEAust haplotypes were placed in the *T. aduncus* group, which was supported by very high bootstrap values (99% and 97% for MP and NJ, respectively). MP and NJ analyses using midpoint rooting (excluding *L. acutus)* resulted in trees with the same general topology (results not shown). Figure 2 shows the unweighted MP tree (length = 206 steps) with MP and NJ bootstrap values for topologies that were concordant between methods.

Discussion

In this study we used sequences of the mtDNA control region of photo-identified resident bottlenose dolphins from Jervis Bay and Port Stephens, southeastern Australia, to determine whether these populations belong to the widespread *T. truncatus* or to *T. aduncus.* We found sequence divergence between southeastern Australian (SEAust) haplotypes and *T. aduncus* to be much lower than between SEAust haplotypes and *T. truncatus.* The former was similar to intraspecific divergence found within other delphinid species (*e.g.,*

northern right whale dolphins, Dizon *et al.* 1994; killer whales, Hoelzel and Dover 1991; and Hector's dolphins, Pichler *et al.* 1998). By contrast, sequence divergence between SEAust haplotypes and *T. truncatus* was similar to other delphinid species pairs (*e.g.*, pantropical spotted and spinner dolphins, Dizon *et al.* 1991; and long-beaked common and northern right whale dolphins, Dizon *et al.* 1994). Additionally, phylogenetic analyses were unambiguous at placing all SEAust haplotypes within a group composed exclusively of *T. aduncus*. Our results strongly indicated that both populations belong to the species *T. aduncus*. This finding greatly extends the range of *T. aduncus* from the Indo-Pacific and Indian Ocean to subtropical waters of the western South Pacific. Moreover, low levels of sequence divergence between *T. aduncus* haplotypes of southeastern Australia and Chinese waters (*e.g.*, SEAust2 and Tadu2) suggest that these coastal populations have diverged recently.

Of further interest is the observation that Jervis Bay and Port Stephens bottlenose dolphins are apparently unspotted, in contrast to previous observations of spotted adult individuals farther north on the east coast of Australia (Ross and Cockcroft 1990; P. Corkeron, personal communication). Over the course of several hundred hours of observation, the ventral surface of adult individuals from both populations was seen at close range on numerous occasions and spotting was not visible (L. Möller, personal observation). Ventral spotting has previously been used to differentiate the *aduncus* and *truncatus* forms in South Africa (Ross 1977), to separate subspecies of *T. truncatus* in Australia (Ross and Cockcroft 1990), and as a diagnostic character of *T. aduncus* in Chinese waters (Wang *et al.* 1999). Ross and Cockcroft (1990) showed that regional variation occurred in the extent of ventral spotting for Australian bottlenose dolphins. They found a cline from unspotted dolphins in the south to spotted in the north on both the east and west coasts (Ross and Cockcroft 1990). Unfortunately, data on ventral spotting for the east coast were restricted to a small number of animals held in captivity. Animals originating from Port Macquarie, 150 km north of Port Stephens, included both unspotted and spotted individuals (Ross and Cockcroft 1990). However, inshore animals captured approximately 400 km further north, in southern Queensland waters, were predominantly spotted (Ross and Cockcroft 1990). It is possible that our study areas in Australia are located south of an area of transition from the spotted to the unspotted form of *T. aduncus,* but further morphological studies are required to clarify this hypothesis.

Ross and Cockcroft (1990) also found latitudinal variation in body length, length and breadth of snout, and skull size of Australian bottlenose dolphins, which they suggest indicate that coastal populations are locally resident. This

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Table 3. Pairwise sequence divergence between haplotypes of bottlenose dolphins from southeastern Australia, and GenBank sequences of *T. aduncus* and *T. truncatus*, and one L. acutus. Mean character differences shown above diagonal and total character differences presented below diagonal. Details of haplotypes presented in Table 1, 2.

	Tadu1	Tadu2	Tadu3	Tadu4	Tadu5	Tadu6	Tadu7	Tadu8	Tadu9	Tadu10	Tadu11	SEAust1	SEAust2	SEAust3	SEAust4	Ttru1	Ttru2	Ttru3	Ttru4	Ttru5
Tadu1		0.022	0.022	0.003	0.022	0.022	0.025	0.025	0.008	0.019	0.027	0.019	0.016	0.016	0.016	0.041	0.060	0.065	0.046	0.068
Tadu2	8		0.011	0.019	0.011	0.011	0.003	0.008	0.025	0.008	0.005	0.008	0.005	0.011	0.005	0.052	0.060	0.055	0.057	0.068
Tadu3	8	4		0.019	0.016	0.011	0.014	0.019	0.025	0.003	0.011	0.014	0.011	0.016	0.011	0.046	0.055	0.055	0.052	0.063
Tadu4	1	7	7		0.019	0.019	0.022	0.022	0.011	0.016	0.025	0.022	0.014	0.019	0.014	0.044	0.057	0.063	0.049	0.065
Tadu5	8	4	6	7		0.011	0.014	0.019	0.025	0.014	0.016	0.014	0.005	0.016	0.011	0.057	0.060	0.065	0.063	0.068
Tadu6	8	4	4	7	4		0.014	0.019	0.025	0.014	0.011	0.014	0.005	0.016	0.011	0.052	0.060	0.060	0.057	0.068
Tadu7	9	1	5	8	5	5		0.011	0.027	0.011	0.003	0.011	0.008	0.014	0.008	0.055	0.063	0.052	0.057	0.071
Tadu8	9	3	7	8	7	7	4		0.022	0.016	0.014	0.016	0.014	0.019	0.008	0.049	0.052	0.046	0.055	0.060
Tadu9	3	9	9	4	9	9	10	8		0.022	0.030	0.022	0.019	0.019	0.019	0.049	0.052	0.057	0.055	0.060
Tadu10	7	3	1	6	5	5	4	6	8		0.014	0.011	0.008	0.014	0.008	0.049	0.057	0.057	0.055	0.065
Tadu11	10	2	4	9	6	4	1	5	11	5		0.014	0.011	0.016	0.011	0.052	0.060	0.049	0.055	0.068
SEAust1	7	3	5	8	5	5	4	6	8	4	5		0.008	0.008	0.008	0.049	0.063	0.063	0.055	0.071
SEAust2	6	2	4	5	2	2	3	5	7	3	4	3		0.011	0.005	0.052	0.060	0.060	0.057	0.068
SEAust3	6	4	6	7	6	6	5	7	7	5	6	3	4		0.016	0.052	0.065	0.060	0.057	0.074
SEAust4	6	2	4	5	4	4	3	3	7	3	4	3	2	6		0.046	0.055	0.055	0.052	0.063
Ttru1	15	19	17	16	21	19	20	18	18	18	19	18	19	19	17		0.027	0.035	0.011	0.035
Ttru2	22	22	20	21	22	22	23	19	19	21	22	23	22	24	20	10		0.024	0.033	0.014
Ttru3	24	20	20	23	24	22	19	17	21	21	18	23	22	22	20	13	9		0.043	0.033
Ttru4	17	21	19	18	23	21	21	20	20	20	20	20	21	21	19	4	12	16		0.041
Ttru5	25	25	23	24	25	25	26	22	22	24	25	26	25	27	23	13	5	12	15	
Ttru6	22	22	20	21	22	22	23	21	21	21	22	23	22	24	20	12	4	13	12	7
Ttru7	23	23	21	22	23	23	24	22	22	22	23	24	23	25	21	13	7	14	15	8
Ttru8	25	25	23	24	25	25	26	22	22	24	25	26	25	27	23	13	5	12	15	2
Ttru9	21	21	19	20	21	21	22	20	20	20	21	22	21	23	19	11	5	12	13	6
Ttru10	25	23	23	24	25	25	24	20	22	24	23	26	25	25	23	13	5	10	15	4
Ttru11	25	21	21	24	25	23	20	18	22	22	19	24	23	23	21	14	10	1	17	13
Ttru12	21	21	19	20	21	21	22	18	18	20	21	22	21	23	19	9	1	10	11	6
Ttru13	23	23	21	22	23	23	24	20	20	22	23	24	23	25	21	11	1	10	13	6
Ttru14	19	19	19	18	23	21	20	18	18	20	19	22	21	21	19	12	11	12	14	16
Ttru15	23	23	21	22	23	21	24	22	22	22	23	24	23	25	21	11	5	12	13	6
Ttru16	21	23	21	22	25	23	24	20	20	22	23	22	23	23	21	8	12	13	12	15
Ttru17	22	22	22	23	26	22	23	19	21	23	22	23	24	22	22	10	14	13	12	17
Ttru18	21	23	21	22	25	23	24	20	20	22	23	22	23	23	21	7	9	12	9	14
Ttru19	20	20	20	21	24	22	21	19	19	21	20	21	22	20	20	7	11	12	11	14
Ttru20	22	24	22	23	26	24	25	21	19	23	24	23	24	24	22	8	8	11	12	11
Ttru21	20	20	18	19	20	20	21	19	19	19	20	21	20	22	18	8	2	9	12	5
Ttru22	19	21	19	20	23	21	22	18	18	20	21	20	21	21	19	8	8	11	10	11
Ttru23	24	22	22	23	24	22	23	19	21	23	22	25	24	24	22	11	3	10	13	8
Ttru24	24	22	22	23	24	22	23	19	21	23	22	25	24	24	22	12	2	9	14	7
L. acutus	38	38	38	39	42	40	38	37	39	39	37	39	40	38	38	34	38	38	35	39

Table 3. Continued.

	Ttru6	Ttru7	Ttru8	Ttru9	Ttru10	Ttru11	Ttru12	Ttru13	Ttru14	Ttru15	Ttru16	Ttru17	Ttru18	Ttru19	Ttru20	Ttru21	Ttru22	Ttru23	Ttru24	L.acutus
Tadu1	0.060	0.063	0.068	0.057	0.068	0.068	0.057	0.063	0.052	0.063	0.057	0.060	0.057	0.055	0.060	0.055	0.052	0.065	0.065	0.105
Tadu2	0.060	0.063	0.068	0.057	0.063	0.057	0.057	0.063	0.052	0.063	0.063	0.060	0.063	0.055	0.065	0.055	0.057	0.060	0.060	0.105
Tadu3	0.055	0.057	0.063	0.052	0.063	0.057	0.052	0.057	0.052	0.057	0.057	0.060	0.057	0.055	0.060	0.049	0.052	0.060	0.060	0.105
Tadu4	0.057	0.060	0.065	0.055	0.065	0.065	0.055	0.060	0.049	0.060	0.060	0.063	0.060	0.057	0.063	0.052	0.055	0.063	0.063	0.108
Tadu5	0.060	0.063	0.068	0.057	0.068	0.068	0.057	0.063	0.063	0.063	0.068	0.071	0.068	0.065	0.071	0.055	0.063	0.065	0.065	0.116
Tadu6	0.060	0.063	0.068	0.057	0.068	0.063	0.057	0.063	0.057	0.057	0.063	0.060	0.063	0.060	0.065	0.055	0.057	0.060	0.060	0.111
Tadu7	0.063	0.065	0.071	0.060	0.065	0.055	0.060	0.065	0.055	0.065	0.066	0.063	0.065	0.057	0.068	0.057	0.060	0.063	0.063	0.105
Tadu8	0.057	0.060	0.060	0.055	0.055	0.049	0.049	0.055	0.049	0.060	0.055	0.052	0.055	0.052	0.057	0.052	0.049	0.052	0.052	0.102
Tadu9	0.057	0.060	0.060	0.055	0.060	0.060	0.049	0.055	0.049	0.060	0.055	0.057	0.055	0.052	0.052	0.052	0.049	0.057	0.057	0.108
Tadu10	0.057	0.060	0.065	0.055	0.065	0.060	0.055	0.060	0.055	0.060	0.060	0.063	0.060	0.057	0.063	0.052	0.055	0.063	0.063	0.108
Tadu11	0.060	0.063	0.068	0.057	0.063	0.052	0.057	0.063	0.052	0.063	0.063	0.060	0.063	0.055	0.065	0.055	0.057	0.060	0.060	0.102
SEAust1	0.063	0.065	0.071	0.060	0.071	0.065	0.060	0.065	0.060	0.065	0.060	0.063	0.060	0.057	0.063	0.057	0.055	0.068	0.068	0.108
SEAust2	0.060	0.063	0.068	0.057	0.068	0.063	0.057	0.063	0.057	0.063	0.063	0.065	0.063	0.060	0.065	0.055	0.057	0.065	0.065	0.111
SEAust3	0.065	0.068	0.074	0.063	0.068	0.063	0.063	0.068	0.057	0.068	0.063	0.060	0.063	0.055	0.065	0.060	0.057	0.065	0.065	0.105
SEAust4	0.055	0.057	0.063	0.052	0.063	0.057	0.052	0.057	0.052	0.057	0.057	0.060	0.057	0.055	0.060	0.049	0.052	0.060	0.060	0.105
Ttru1	0.033	0.035	0.035	0.030	0.035	0.038	0.024	0.030	0.033	0.030	0.022	0.027	0.019	0.019	0.022	0.022	0.022	0.030	0.033	0.094
Ttru2	0.011	0.019	0.014	0.014	0.014	0.027	0.003	0.003	0.030	0.014	0.033	0.038	0.024	0.030	0.022	0.005	0.022	0.008	0.005	0.105
Ttru3	0.035	0.038	0.033	0.033	0.027	0.003	0.027	0.027	0.033	0.033	0.035	0.035	0.033	0.033	0.030	0.024	0.030	0.027	0.024	0.105
Ttru4	0.033	0.041	0.041	0.035	0.041	0.046	0.030	0.035	0.038	0.035	0.033	0.033	0.024	0.030	0.033	0.033	0.027	0.035	0.038	0.096
Ttru5	0.019	0.022	0.005	0.016	0.011	0.035	0.016	0.016	0.043	0.016	0.041	0.046	0.038	0.038	0.030	0.014	0.030	0.022	0.019	0.107
Ttru6		0.008	0.019	0.003	0.019	0.038	0.014	0.014	0.030	0.014	0.044	0.049	0.035	0.030	0.033	0.011	0.033	0.019	0.016	0.099
Ttru7	3		0.022	0.005	0.016	0.035	0.022	0.016	0.038	0.016	0.046	0.052	0.043	0.033	0.035	0.014	0.035	0.027	0.024	0.102
Ttru8	7	8		0.016	0.016	0.035	0.016	0.016	0.043	0.016	0.041	0.046	0.038	0.038	0.030	0.014	0.030	0.022	0.019	0.107
Ttru9	1	2	6		0.016	0.035	0.016	0.016	0.033	0.011	0.041	0.046	0.038	0.027	0.030	0.008	0.030	0.022	0.019	0.096
Ttru10	7	6	6	6		0.024	0.016	0.011	0.038	0.016	0.041	0.041	0.038	0.033	0.030	0.014	0.030	0.016	0.014	0.107
Ttru11	14	13	13	13	9		0.030	0.024	0.035	0.035	0.038	0.038	0.035	0.035	0.033	0.027	0.033	0.030	0.027	0.107
Ttru12	5	8	6	6	6	11		0.005	0.027	0.016	0.035	0.041	0.027	0.033	0.024	0.008	0.024	0.011	0.008	0.102
Ttru13	5	6	6	6	4	9	2		0.033	0.016	0.035	0.041	0.027	0.033	0.024	0.008	0.024	0.011	0.008	0.107
Ttru14	11	14	16	12	14	13	10	12		0.038	0.044	0.043	0.035	0.035	0.038	0.030	0.041	0.030	0.030	0.099
Ttru15	5	6	6	4	6	13	6	6	14		0.035	0.038	0.033	0.030	0.024	0.008	0.030	0.016	0.014	0.107
Ttru16	16	17	15	15	15	14	13	13	16	13		0.025	0.014	0.027	0.016	0.033	0.022	0.035	0.038	0.105
Ttru17	18	19	17	17	15	14	15	15	16	14	9		0.016	0.022	0.019	0.038	0.016	0.030	0.033	0.099
Ttru18	13	16	14	14	14	13	10	10	13	12	5	6		0.019	0.014	0.030	0.019	0.027	0.030	0.102
Ttru19	11	12	14	10	12	13	12	12	13	11	10	8	7		0.022	0.024	0.030	0.027	0.030	0.096
Ttru20	12	13	11	11	11	12	9	9	14	9	6	7	5	8		0.022	0.011	0.024	0.027	0.099
Ttru21	4	5	5	3	5	10	3	3	11	3	12	14	11	9	8		0.022	0.014	0.011	0.099
Ttru22	12	13	11	11	11	12	9	9	15	11	8	6	7	11	4	8		0.030	0.027	0.094
Ttru23	7	10	8	8	6	11	4	4	11	6	13	11	10	10	9	5	11		0.003	0.102
Ttru24	6	9	7	7	5	10	3	3	11	5	14	12	11	11	10	4	10	1		0.105
L. acutus	36	37	39	35	39	39	37	39	36	39	38	36	37	35	36	36	34	37	38	

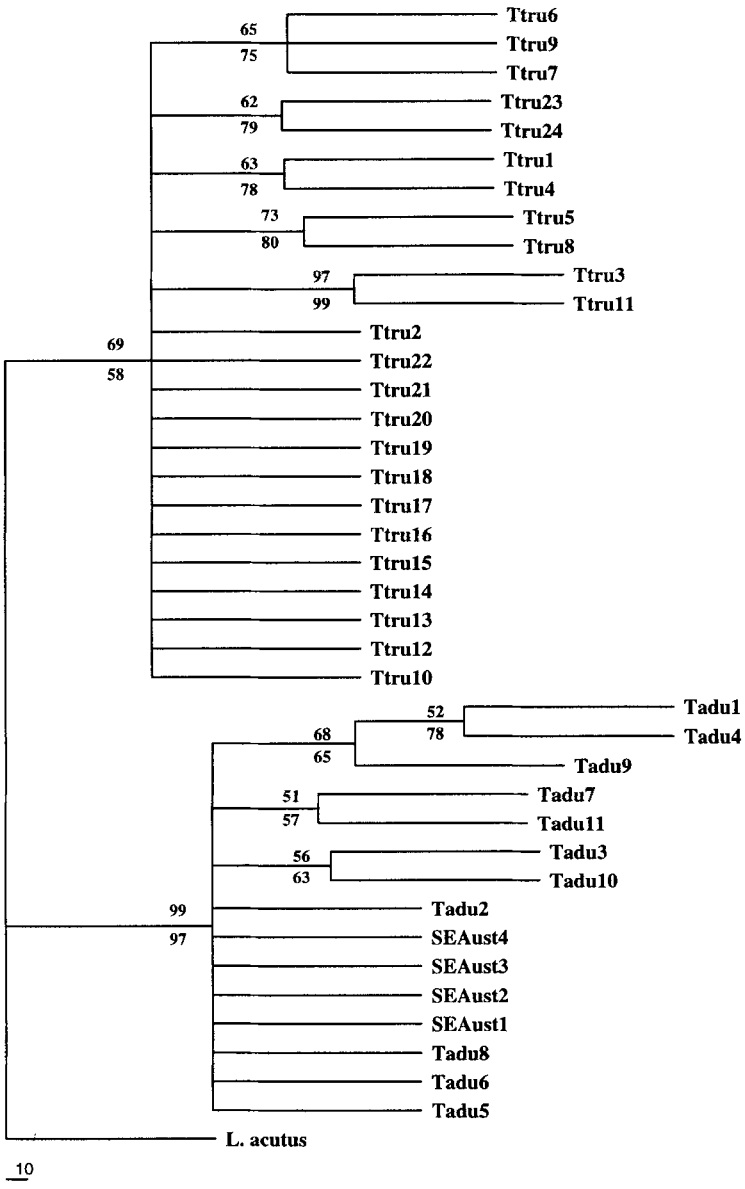

Figure 2. Maximum parsimony tree based on sequences of mtDNA control region of bottlenose dolphins from southeastern Australia, and published *T. aduncus* (Tadu) and *T. truncatus* (Ttru) from different localities (50% majority-rule consensus tree). Branch lengths are proportional to number of changes (scale corresponds to 10 changes). Maximum parsimony and neighbor-joining bootstrap supports shown above and below branches, respectively. Details of haplotypes are presented in Table 1, 2. *L. acutus* used as outgroup.

hypothesis is supported by our own photo-identification studies in Jervis Bay and Port Stephens, where most identified dolphins have been observed year-round (Möller and Harcourt 1998; L. Möller, unpublished data). However, Ross and Cockcroft (1990) concluded that there was no species-level morphological differentiation within their sample. Based on this conclusion and our results, we believe that *T. aduncus* may be continuously distributed in coastal waters around Australia. Nonetheless, Ross and Cockcroft (1990) also reported marked differences in body size between inshore and offshore bottlenose dolphins in southern Queensland, which in contrast may suggest that the occurrence of *T. truncatus* in Australian offshore waters cannot be discarded. The presence of many diagnostic sequence differences between *T. truncatus* and *T. aduncus* implies that analysis of the mtDNA control region may be a rapid approach to further investigate the distribution of these species in Australia and elsewhere.

Finally, coastal bottlenose dolphin populations, such as the ones in Jervis Bay and Port Stephens, are the targets of a rapidly growing dolphin-watch industry in Australia. Photo-identification and mark-resight studies in these areas have shown that both populations are resident and relatively small, and microsatellite data also suggest that they are genetically differentiated at the nuclear DNA level (Möller and Harcourt 1998; L. Möller, unpublished data). Because small populations are generally more vulnerable to the effects of demographic and environmental stochasticity, genetic drift, and inbreeding (Caughley 1994), it is important to define population boundaries and stock structure of *T. aduncus* in Australia to develop effective management actions.

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