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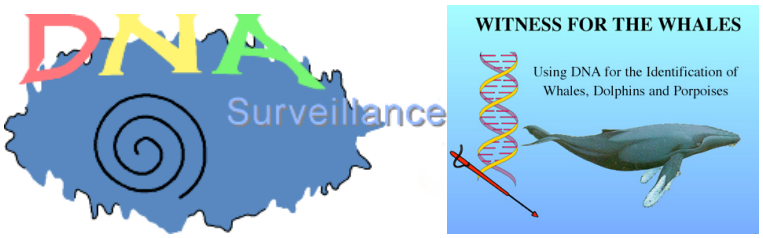

Witness for the whales, Vs 4.3: a comprehensive and evaluated dataset of DNA sequences for improved molecular taxonomy and identification of cetacean species

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Background

DNA sequences of homologous loci provide universal characters for identification of species. Such genetic characters are particularly useful for groups such as cetaceans, in which morphological features are subtle and difficult to compare because of rarity of specimens or widespread distributions. The use of genetic databases to identify cetacean products for purposes of monitoring trade and investigating illegal hunting or for identifying ambiguous beachcast specimens has become common. More recently, there has been a general recognition of the value of systematic application of molecular genetic identification to basic organismal taxonomy. In cetaceans, this has lead to the recent discovery of a new species of beaked whale, *Mesoplodon perrini* (Dalebout et al. 2002), and the recognition of species- or subspecies-level subdivisions among several taxa previously considered monotypic, e.g. Irrawaddy dolphins (Beasely et al. 2005), the South American coastal and riverine dolphins *Sotalia* (Caballero et al. in press), common dolphins (Rosel et al. 1994), 'bottlenose' dolphins (Wang et al. 1999; LeDuc et al 1999), Amazon river dolphins (*Inia*, Banguera-Hinestroza, 2002), Hector's dolphins (A. Baker et al. 2002), right whales (Rosenbaum et al. 2000), Bryde's whales (Wada et al. 2003) and minke whales (Baker et al. 2000). DNA-based taxonomic identification is likely to reveal further taxonomic divisions important to conservation, especially where local populations are threatened by direct exploitation. Further, documentation and eventual regulation of cetacean exploitation around the world would be greatly improved by accurate species identification from tissue samples collected from market surveys and during fisheries operations (e.g., Baker et al. 2006; Endo et al. 2005).

The Web-based program, *DNA Surveillance* is an online tool for species identification using DNA sequence data and phylogenetic analysis (Ross et al. 2003) available at www.dna-surveillance.auckland.ac.nz. The application aligns a user-submitted 'query' or 'test' sequence of unknown origin against a dataset of 'reference' sequences representing a particular taxonomic group of interest. The evolutionary distances between the query sequence and each of the reference sequences are computed and a phylogenetic tree displays the affinity of the query sequence to the reference sequences (Ross et al. 2003; Baker et al. 2003). *DNA Surveillance* differs in several important ways from the BLAST search options available on the website of the international genetic database, GenBank. Sequences in GenBank often are not associated with identifiable reference or voucher specimen material. Further, the taxonomic representation of a BLAST search is difficult to judge because of the large number of redundant gene

sequences for some species, the absence of sequences from other closely related species and the nature of the pairwise alignment and search algorithm. To address these deficiencies, the reference sequences in *DNA Surveillance* are prealigned at each hierarchical level of the database, using a mixture of algorithmic and manual methods, to assure an optimized alignment for the submitted test sequence.

The flagship application of *DNA Surveillance* has been to improve the molecular taxonomy of whales, dolphins and porpoises through implementation of a comprehensive reference database, *Witness for the Whales* (Baker et al. 2003). At the time of this contract proposal, the reference dataset (Version 3.1) implemented on www.DNA-surveillance included 285 sequences of the mtDNA control region or Dloop, representing 78 cetacean species, and 165 sequences of the mtDNA cytochrome *b* gene representing 83 cetacean species. However, some of these sequences were unpublished or poorly documented. Here, we report on progress to date in improving the reliability and accuracy of taxonomic identification by DNA *S*urveillance through modification of the application and evaluation of expanded comprehensive reference datasets for cetaceans. Datasets for other taxa, including some protected under international agreement, are under development.

• Goals and Objectives

The specific objectives of the contract proposal followed recommendations from the *Symposium and Workshop on Cetacean Systematics* (Reeves et al. 2004), including:

1) To complete assembly of comprehensive datasets of mitochondrial (mt) DNA control region (or Dloop) and cytochrome *b* (cytB) sequences from all known species of cetaceans (approximately 87 species), with a minimum representation for the control region of 2-6 individuals for each species and, where possible, 2-6 individuals for each regional stock or oceanic population;
2) To 'evaluate' all reference sequences in the datasets, following the criteria discussed in Dizon et al. (2000), to reduce the likelihood of errors and improve documentation of source material (e.g., skeletal material or photographs of the specimen);
3) To mount the comprehensive datasets as Version 4.0 on the web-based application for species identification, www.DNA-surveillance, and to modify the application to allow downloading of the aligned 'query' sequence and selected reference datasets for subsequent user analysis;
4) To publish a description of the comprehensive dataset, with the criteria for evaluating the reference samples, and submit all unpublished sequences from the comprehensive reference dataset to the international genetic archives, GenBank and EMBL;
5) To initiate electronic curation (E-curation) of datasets, as a means of facilitating administration of dataset from wide-spread species, such as humpback whales or *Tursiops* spp.;
6) To develop linkages for www.DNA-surveillance with other web-based programs for Census for Marine Life, OBIS and explore potential for integration of genetic identification and geographic location of source reference through SEAMAP.

Database update

Witness for the Whales, database Vs3.1 has been revised by replacing all sequences of unknown provenance with those of known provenance, keeping the original number of 285 sequences of the mtDNA control region, representing 78 species, and 165 sequences of the mtDNA cytochrome *b* gene representing 83 cetacean species. A total of 47 new control region sequences have been submitted to GenBank (Appendix 1) and all sequences in the CytB dataset of Vs3.1 are already available in GenBank. The aligned sequences for each of the eight Vs3.1 datasets can now be downloaded from *DNA Surveillance* for further user-based analyses (e.g., analysis of characters or phylogenetic reconstruction by Maximum Parsimony or Maximum Likelihood).

Witness for the Whales, database Vs 4.3 is now taxonomically comprehensive, with a total of 399 control region sequences and 264 cyt *b* sequences representing 88 species (Table 1). Sequences from documented specimens now represent all of the 83 species recognized by Rice (1998), with two exceptions: the Atlantic hump-backed dolphin, *Sousa teuszi* and the Indian hump-backed dolphin *S. plumbea* (the latter of which has not accepted by IWC). We have also included seven species proposed in recent publications and three subspecies of baleen whales (Table 1). Both the control region and cytB datasets include unique sequences from 2-6 specimens for most species. The few exceptions include unusual cases like the vaquita, which has only a single known mtDNA haplotype. For widespread species, we have included control region sequences from representatives of different ocean basins or biogeographic zones, following the regional categories used in the archive listings of the NMFS Southwest Fisheries Science Center.

Both Vs 4.3 and Vs 3.1 are arranged hierarchically into eight datasets, allowing a progressive increase in species resolution while providing relatively efficient computation (Fig. 1). Both Vs 4.3 and Vs 3.1 are available on *DNA Surveillance* for use in phylogenetic identification but sequences in Vs 4.3 are not downloadable, as some remain proprietary. The documentation of each sequence has been greatly improved with locality and institutional references available in most cases. Appendix 2 gives an example of documentation for the family-specific dataset of cytB sequences for 50 specimens representing all 21 recognized species of beaked whales (Ziphiidae Vs4.3, Dalebout et al. 2004). 'Species-specific' datasets of control region sequences have been compiled for the humpback whale and for the right and bowhead whales (Vs4.0).

Program updates

DNA Surveillance has been totally reprogrammed to include numerous improvements:

i) The security of the site has been improved, and is now password protected at several levels;
ii) The reprogrammed site allows 'delegated administration' of reference datasets for the purposes of improved 'E-curation'. This modification allows curation of individual datasets (e.g. species specific datasets), within a larger dataset, as well as the addition of datasets from other taxonomic groups;
iii) The administrator now has the option of allowing or denying the download of aligned test and reference sequences for the purposes of user-directed analyses (now implemented for database version Vs3.1);
iv) Although outside of the specific scope of this contract, it is worth noting that the beta site now includes preliminary reference databases for six other taxonomic groups, including sea horses, a group recently placed under control of the Convention on International Trade in Endangered Species (CITES).

Review of GenBank cetacean sequences

GenBank and the interlinked DNA Data Bank of Japan and the European Molecular Biology Laboratory nucleotide database (EMBL) are the primary public repositories for genetic information. However, the accuracy of sequences has generally been the responsibility of the individual depositor and concerns have been raised about the quality of submitted sequences or their documentation at a number of levels. These uncertainties have consequences for species identification via BLAST or when sequences are downloaded and used in individual phylogenetic studies.

To investigate the potential for error in either GenBank or the *Witness for whale* reference datasets, associate investigator Howard Ross undertook an extensive cross-validation of the two sources (Ross and Murugan 2006). The validation exercise used GenBank release #143 (August-September 2004) and *Witness for the Whales* Vs3.1 and was completed prior to the submission of the previously unpublished sequences in July 2005. A total of 1,609 mtDNA control region sequences were selected for analysis of which 1,339 had been labeled in GenBank as being of cetacean origin, and 270 of non-cetacean origin. All of the sequences labeled as non-cetacean by GenBank were recognized as non-cetacean by DNA Surveillance and rejected. Of the sequences labeled as cetaceans, 94% were identified in DNA Surveillance to the correct source species, and of these, two-thirds were identified with 'strong evidence' rather than only 'moderate evidence'. Overall, the two systems showed good agreement in positive (cetacean ID) and negative (non-cetacean ID) outcomes. Disagreement occurred for only a small number of sequences. Conflicting identifications arose from differences in nomenclature and taxonomy (due to the absence of taxonomic review within GenBank), and a few cases of apparent species misidentification or true paraphyly among members of the family Delphinidae (i.e., sharing of mtDNA lineages across accepted species). A similar result was found in the cross-validation of cytochrome *b* sequences (Ross and Murugan 2006). For both loci, it was noted that the taxonomic coverage of GenBank was incomplete and that many species of cetaceans were not represented in the database or were represented by only a small number of samples from a limited geographic range of the species.

Improved cetacean species identification

Improvements in species identification using *Witness for the Whales* Vs4.3 and the updated version of *DNA Surveillance* is evidenced by results from recent surveys of Japanese and Korean markets. In Japan (Endo et al. 2005), a total of 160 'small cetacean' products sold for human consumption in markets from 2000 to 2003 were identified as originating from nine species: false killer whale, bottlenose dolphin, short-finned pilot whale, striped dolphin, rough-toothed dolphin, Risso's dolphin, pantropical spotted dolphin, Baird's beaked whale, and Dall's porpoise. Ambiguity was encountered only in products that were identified as 'likely striped dolphins' as a result of the high diversity and possible paraphyly (see above) found among some species of *Stenella* and *Delphinus.* In Korea (Baker et al. 2006), a total of 357 'whalemeat' products, purchased from late 2003 to early 2005, were identified unambiguously as originating from 15 species of cetaceans: three species of baleen whales (North Pacific minke, common form Bryde's and humpback), three species of beaked whales (Cuvier's, Stejneger's and Blainville's), seven species of dolphins (short-finned pilot, false killer and killer whales; Risso's, bottlenose, common and Pacific white-sided dolphins) and two species of porpoises (harbor and finless).

Linkages with other web-based programs

Communication is ongoing with investigators involved in other Web-based or molecular taxonomic initiatives, including the Census of Marine Life and the Consortium for the (DNA) Barcode of Life. In this regard, associate investigator Shane Lavery attended a workshop, *DNA Barcoding for the Census of Marine Life*, in May, 2006 at the Netherlands Royal Academy of Arts and Sciences, in Amsterdam and reported on the application *DNA Surveillance.* The DNA Barcoding consortium has focused on the use of a single gene, the mtDNA cytochrome oxidase I (COI), for the identification of all animal species. Although the methodology of the program *DNA Surveillance* is fully compatible with use of the COI gene or other loci, our efforts to generate reference datasets have focused on the mtDNA control region and cytochrome *b* genes as primary candidates for identification of cetaceans. Conforming to the protocol of the DNA Barcoding consortium will require additional effort, particularly in regards to obtaining access to rare specimens. Further study would be useful to evaluate the taxon-specific accuracy of cetacean species identification by different mitochondrial or nuclear genes and to inform the emerging concensus on molecular taxonomy.

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Table 1: Total species and representative sequences for each of the two mtDNA genes (control region and cytochrome *b*) included in Version 4.3 of the reference database in DNA surveillance. Accepted species follow Rice (1998). Newly accepted or proposed species: *Balaenoptera omurai, Eubalaena australis, Eubalaena japonicus, Mesoplodon perrini, Orcaella heinsohni, Platanista minor, Sotalia guinensis*. Subspecies: *Balaenoptera acutorostrata subsp, Balaenoptera musculus brevicauda, Balaenoptera acutorostrata scammoni*. Regions: NP North Pacific, SP South Pacific, NA North Atlantic, SA South Atlantic, IO, Indian Ocean, ETP Eastern Tropical Pacific.

Species code	Species name	Common name	Dlp	Region	Cyt B	Region
Adio	*Phocoena dioptrica*	spectacled porpoise	1		3	
Bacu	*Balaenoptera acutorostrata acutorostrata*	North Atlantic minke whale	3		1	
	Balaenoptera acutorostrata scammoni	North Pacific minke whale	3		3	
BacDW	*Balaenoptera acutorostrata subsp.*	dwarf minke whale	2		1	
Barn	*Berardius arnuxii*	Arnoux's beaked whale	6		2	
Bbar	*Berardius bairdii*	Baird's beaked whale	6		2	
Bbon	*Balaenoptera bonaerensis*	Antartic minke whale	4		4	
Bbor	*Balaenoptera borealis*	sei whale	3		2	
Bomu	*Balaenoptera omurai*	Bryde's whale (Solomon Islands form)	2		1	
Bede	*Balaenoptera edeni*	Bryde's whale (Kochi form)	3		1	
Bbry	*Balaenoptera brydei*	Bryde's whale (common form)	3		3	
Bmus	*Balaenoptera musculus*	blue whale	2		2	
Bmus pygmy	*Balaenoptera musculus brevicauda*	pygmy blue whale	2		1	
Bmys	*Balaena mysticetus*	bowhead whale	6		2	
Bphy	*Balaenoptera physalus*	fin whale	2		3	
Ccom	*Cephalorhynchus commersonii*	Commerson's dolphin	6		2	
Ceut	*Cephalorhynchus eutropia*	Chilean dolphin	6		3	
Chea	*Cephalorhynchus hectori*	Hector's dolphin	6		2	
Chec	*Cephalorhynchus heavisidii*	Heaviside's dolphin	6		3	
Cmar	*Caperea marginata*	pygmy right whale	2		2	
Dcap	*Delphinus capensis*	common dolphin (long-beaked)	7		2	
Dtro	*Delphinus tropicalis*	common dolphin (Arabian)	2		1	
Ddel	*Delphinus delphis*	common dolphin (short-beaked)	3	NP	5	
			1	ETP		
			4	NA		
Dleu	*Delphinapterus leucas*	beluga whale	2		2	
Eaus	*Eubalaena australis*	southern right whale	6		2	
Egla	*Eubalaena glacialis*	north Atlantic right whale	5		4	
Ejap	*Eubalaena japonicus*	north Pacific right whale	6		4	
Erob	*Eschrichtius robustus*	Gray whale	6		5	
Fatt	*Feresa attenuata*	pygmy killer whale	5		3	
Ggri	*Grampus griseus*	Risso's dolphin	6		7	
Gmac	*Globicephala macrorhynchus*	short finned pilot whale	1	NA	3	
			1	NP		
			1	ETP		
			4	SP		
Gmel	*Globicephala melas*	long finned pilot whale	4		3	
Hamp	*Hyperodon ampullatus*	northern bottlenose whale	5		2	
Hpla	*Hyperodon planifrons*	southern bottlenose whale	6		2	

Igeo	*Inia geoffrensis*	Amazon river dolphin	3	6
Ipac	*Indopacetus pacificus*	Longman's beaked whale	5	5
Kbre	*Kogia breviceps*	pygmy sperm whale	1 NP 1 NA 2 SA 2 SP	6
Ksim	*Kogia sima*	dwarf sperm whale	6	2
Lacu	*Lagenorhynchus acutus*	Atlantic white-sided dolphin	2	2
Lalb	*Lagenorhynchus albirostris*	white-beaked dolphin	2	4
Laus	*Lagenorhynchus australis*	Peale's dolphin	3	3
Lbor	*Lissodelphis borealis*	northern right whale dolphin	4	2
Lcru	*Lagenorhynchus cruciger*	hourglass dolphin	3	4
Lhos	*Lagenodelphis hosei*	Fraser's dolphin	2 NP 4 NA	7
Lobl	*Lagenorhynchus obliquidens*	Pacific white-sided dolphin	4	3
Lobs	*Lagenorhynchus obscurus*	dusky dolphin	2 SP (Peru) 4 SP (NZ)	5
Lper	*Lissodelphis peronii*	southern right whale dolphin	2	2
Lvex	*Lipotes vexillifer*	Yangtze river dolphin	4	2
Mbid	*Mesoplodon bidens*	Sowerby's beaked whale	6	2
Mbow	*Mesoplodon bowdoini*	Andrews' beaked whale	5	2
Mcar	*Mesoplodon carlhubbsi*	Hubb's beaked whale	7	2
Mden	*Mesoplodon densirostris*	Blainville's beaked whale	6	2
Meur	*Mesoplodon europaeus*	Gervais' beaked whale	5	2
Mgin	*Mesoplodon ginkgodens*	Ginkgo-toothed beaked whale	5	2
Mgra	*Mesoplodon grayi*	Gray's beaked whale	6	2
Mhec	*Mesoplodon hectori*	Hector's beaked whale	6	2
Mlay	*Mesoplodon layardii*	strap-toothed beaked whale	6	2
Mmir	*Mesoplodon mirus*	True's beaked whale	4	2
Mmon	*Monodon monoceros*	Narwhal	2	2
Mnov	*Megaptera novaeangliae*	humpback whale	2	2
Mper	*Mesoplodon peruvianus*	pygmy beaked whale	3	2
Mpir	*Mesoplodon perrini*	Perrin's beaked whale	5	5
Mste	*Mesoplodon stejnegeri*	Stejneger's beaked whale	6	2
Mtra	*Mesoplodon traversii*	Spade-toothed beaked whale	3	3
Npho	*Neophocaena phocaenoides*	finless porpoise	8	2
Obre	*Orcaella brevirostris*	Irrawaddy dolphin	2	2
Ohei	*Orcaella heinsohni*	snubfin dolphin	1	1
Oorc	*Orcinus orca*	killer whale	1 SO 1 NA 1 NP 5 SP	6
Pbla	*Pontoporia blainvillei*	Franciscana	2	3
Pcra	*Pseudorca crassidens*	false killer whale	2	4
Pdal	*Phocoenoides dalli*	Dall's porpoise	6	4
Pele	*Peponocephala electra*	melon-headed whale	2 SP 1 NP 3 NA	5
Pgan	*Platanista gangetica*	Ganges river dolphin	3	3
Pmac	*Physeter macrocephalus*	sperm whale	2	3
Pmin	*Platanista minor*	Indus river dolphin	3	3
Ppho	*Phocoena phocoena*	harbour porpoise	3 NA	3

			3 3	NP Black Sea	
Psin	*Phocoena sinus*	Vaquita	1		2
Pspi	*Phocoena spinipinnis*	Burmeister's porpoise	6		3
Satt	*Stenella attenuata*	pantropical spotted dolphin	3		3
Sbre	*Steno bredanensis*	rough-toothed dolphin	2		4
Schi	*Sousa chinensis*	Indo-Pacific humpback dolphin	6		7
Scly	*Stenella clymene*	Clymene dolphin	4		2
Scoe	*Stenella coeruleoalba*	striped dolphin	3		4
Sflu	*Sotalia fluviatilis*	Tucuxi	1		1
Sgui	*Sotalia guinensis*	Costero	1		1
Sfro	*Stenella frontalis*	Atlantic spotted dolphin	6		6
Slon	*Stenella longirostris*	spinner dolphin	2 4	NA SP	4
Tadu	*Tursiops aduncus*	Indo-Pacific bottlenose dolphin	3 4	SP NP	2
Tshe	*Tasmacetus shepherdii*	Shepherd's beaked whale	5		3
Ttru	*Tursiops truncatus*	bottlenose dolphin	3 1 1 3	NA SP (NZ) SP (Kiribati) NP	4
Zcav	*Ziphius cavirostris*	Cuvier's beaked whale	6		2
TOTAL			**399**		**264**