

Research Progress Report for International Whaling Commission Small Cetacean Fund

Defining the units of conservation and historic population dynamics for two small cetacean species affected by directed and incidental catches in the North Pacific

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7 May 2014**Introduction**

Risso's dolphins (*Grampus griseus*) and Fraser's dolphins (*Lagenodelphis hosei*) have been commonly reported in incidental catches and small-scale whaling in many North Pacific regions of Asian coastal waters (Perrin *et al.* 2005, Chou 2006, Kasuya 2007, Chen *et al.* 2011, Robards and Reeves 2011, Carretta *et al.* 2012), however quantitative evaluation of the impact and strategies for mitigation are rarely applied to these species due to the lack of sufficient scientific knowledge on their population structure, population size and demographic trends in this region. The objectives of this research project are to identify genetic stocks for management, investigate patterns of connectivity and the possibility of directional gene flow, and assess evidence for population expansion or decline. A further objective was to assess the species identity of a group of dolphin samples seized from a fish market in southern Taiwan. The specific objectives we proposed to IWC Small Cetacean Fund were:

1. To assess the population structure in Fraser's and Risso's dolphins in the North Pacific and the pattern of connectivity among con-specific regional populations. Funding will permit the incorporation of 45 Risso's and 47 Fraser's dolphins from Taiwan into the broader study;
2. To assess current genetic diversity level for local populations, effective population size, and historical demographic trends;
3. To assess the sampling origin, genetic and phenotypic characters of the group of 'Fraser's dolphins' which was confiscated from an illegal whaling fishery in Ping Dong, Taiwan in 2005. This will be based on multiple loci, incorporated into delphinid sequence data available on public databases;
4. To interpret these results in the context of available data on environmental factors and on historical/ongoing anthropogenic impact, and to prepare a conservation management plan for distribution to regional governmental authorities.

This progress report provides an outline of the results available to date. Specific objectives 1 and 2 are covered by Sections A) Risso's Dolphin and B) Fraser's Dolphin. Objective 3 is covered by Section C) 'Pingdong' Dolphin Identification, and objective 4 by the last section, D) Public Engagement. A final report for this research is due in June, 2014. The materials and methods for conducting this project were provided in the funding application proposal and will be described in the final report, but for brevity are not presented here.

Section A. Risso's dolphins

Table A.1 and Figure A.1 showed the numbers and origins of the samples acquired for this project. The total number of the specimen sampled was 289 and the sampling range principally covered the overall distribution of Risso's dolphin in the North Pacific Ocean. The results presented here include 183 samples for microsatellite and 137 for mitochondrial DNA (mtDNA) sequence analyses.

Table A.1: Numbers and origins of the samples. See Figure A.1 for location definition.

Location	Sampling period	n	n by sampling methods				n by analyses	
			Biopsy	Stranding	Bycatch	Direct catch/ Captive	Micro-satellite	mtDNA
ETP	1998-2007	24	23		1		23	21
NEP	1981-2011	98	41	22	35		77	23
NWP	1986-2010	115		38	2	75 [#]	34	50
WTP	1992-2013	52		15	37		49	43

[#]: None of these were included in the microsatellite analyses

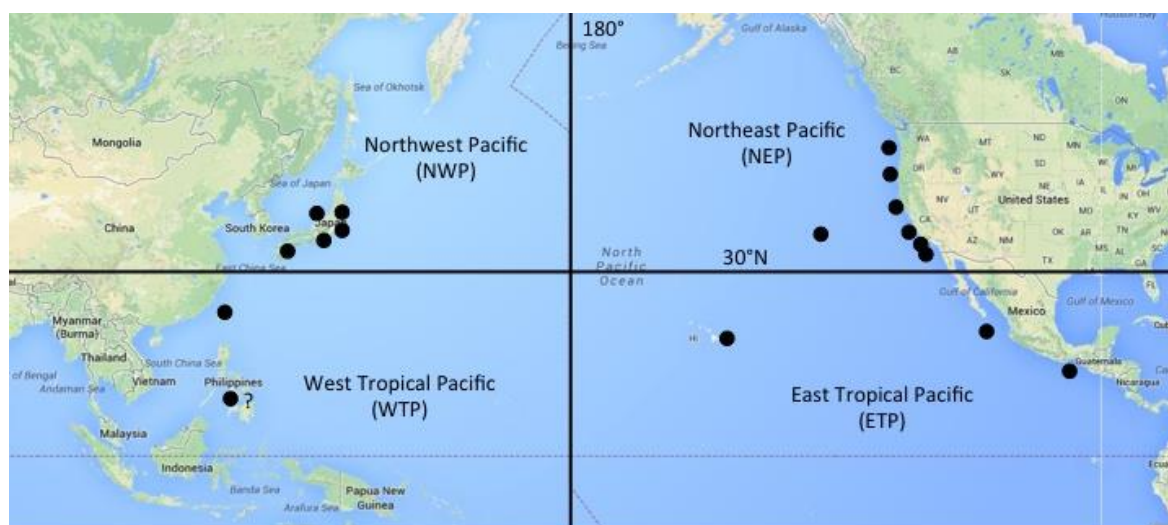


Figure A.1: Map of the approximate sampling locations. Samples were assigned into four groups by geographic features, Northwest Pacific (NWP), West Tropical Pacific (WTP), Northeast Pacific (NEP) and East Tropical Pacific (ETP) by 30°N and 180°. See Table A.1 for the number of samples from each location.

So far 24 microsatellite loci have been applied for all samples; 20 of them had less than 10% missing amplifications ('reliable loci'). Two of those reliable loci are monomorphic (i.e., no variation among all samples) and therefore were excluded from the analyses, leaving 18. Basic statistics for the genetic analyses, including mtDNA genetic diversity, microsatellite allele range, observed and expected heterozygosity are shown in Tables A.2 and A.3. For microsatellite analyses a few loci showed a significant deviation from Hardy-Weinberg Equilibrium (i.e., D22, Dde59, Dde65, Dde69 and KWM2b in various populations) but there was no consistent pattern (see Table A.3), no significance after Bonferroni correction, and their omission did not change inference. Therefore they were retained for the analyses presented.

Table A.2. Results of genetic diversity and estimates of Tajima's D and Fu's F_s from mtDNA analysis. None of the Tajima's D and Fu's F_s estimates were statistically significant (all $P > 0.05$).

	All samples	NWP	WTP	NEP	ETP
# of sequences	137	50	43	23	21
# OF sites	473	473	473	473	473
# of Variable sites (S)	47	36	28	31	27
Total # of mutations (Eta)	47	36	28	31	27
# of haplotypes	55	25	15	15	11
Gene diversity (h)	0.96	0.93	0.90	0.96	0.88
SD of h	0.01	0.03	0.02	0.02	0.06
Nucleotide diversity (Pi)	1.60%	1.47%	1.35%	1.88%	1.71%
SD of Pi	0.07%	0.09%	0.10%	0.14%	0.22%
Average # of nucleotide differences (k)	7.53	6.97	6.39	8.88	8.10
Theta (per sequence) from S, Theta W	8.56	8.04	6.47	8.40	7.50
Theta (per site) frm S, Theta W	0.02	0.02	0.01	0.02	0.02
Tajima's D	-0.37	-0.45	-0.04	0.22	0.30
Fu and Li's D	-0.61	-1.33	-0.10	0.34	0.81
Fu and Li's F	-0.61	-1.21	-0.10	0.36	0.77
Fu's F_s	-28.87	-6.92	-0.61	-2.17	0.16
Strobeck's S	1.00	1.00	0.77	0.96	0.65

Table A.3. Statistics for microsatellite allele numbers, allele range, observed and expected heterozygosity and Hardy-Weinberg Equilibrium test results. Loci in red show significant HWE deviation at the $p < 0.05$ level.

Locus#	ETP								NEP							
	#Genot	#alleles	Allelic range	Obs.Het.	Exp.Het.	P-value	s.d.		#Genot	#alleles	Allelic range	Obs.Het.	Exp.Het.	P-value	s.d.	
AAT44	23	3	9	0.22	0.20	1.00	0.00%		76	3	9	0.37	0.34	0.11	0.03%	
D14	23	9	10	0.91	0.85	0.84	0.03%		77	12	13	0.79	0.83	0.34	0.04%	
D22	23	7	7	0.74	0.84	0.62	0.05%		75	10	11	0.72	0.82	0.05	0.02%	
Dde59	23	12	25	0.74	0.88	0.04	0.02%		77	16	16	0.78	0.85	0.23	0.03%	
Dde65	23	5	8	0.57	0.67	0.04	0.02%		77	6	10	0.70	0.75	0.63	0.05%	
Dde66	23	10	15	0.74	0.83	0.14	0.03%		77	9	16	0.69	0.79	0.26	0.03%	
Dde69	23	9	16	0.74	0.84	0.23	0.05%		76	9	16	0.80	0.81	0.69	0.04%	
Dde70	23	11	13	0.78	0.82	0.36	0.03%		77	15	17	0.73	0.74	0.28	0.02%	
Dde72	23	18	31	0.96	0.94	0.99	0.01%		77	21	44	0.92	0.90	0.82	0.02%	
Dde84	23	6	5	0.87	0.73	0.82	0.04%		77	9	9	0.66	0.72	0.07	0.02%	
EV37	23	10	12	0.65	0.81	0.26	0.03%		75	8	8	0.79	0.76	0.09	0.03%	
KWM2b	23	5	5	0.65	0.71	0.85	0.03%		75	5	5	0.48	0.59	0.03	0.02%	
KWM9b	23	8	8	0.83	0.83	0.56	0.04%		77	12	16	0.83	0.83	0.66	0.03%	
MK3	23	8	9	0.87	0.83	0.80	0.04%		76	9	10	0.87	0.83	0.51	0.04%	
MK5	23	8	8	0.65	0.61	0.89	0.04%		77	10	13	0.73	0.71	0.39	0.04%	
Sco11	23	6	10	0.87	0.79	0.60	0.05%		77	8	18	0.77	0.79	0.22	0.04%	
Sco28	23	1	NA	NA	NA	NA	NA		77	3	9	0.03	0.03	1.00	0.00%	
Sco55	23	4	3	0.22	0.21	1.00	0.00%		77	4	3	0.18	0.19	0.41	0.05%	
Mean		8.176	11.412	0.71	0.73					9.389	13.500	0.66	0.68			
s.d.		3.557	7.194	0.21	0.21					4.667	8.719	0.24	0.24			

Locus#	WTP								NWP							
	#Genot	#alleles	Allelic range	Obs.Het.	Exp.Het.	P-value	s.d.		#Genot	#alleles	Allelic range	Obs.Het.	Exp.Het.	P-value	s.d.	
AAT44	48	4	9	0.25	0.23	1.00	0.00%		34	5	10	0.32	0.29	1.00	0.00%	
D14	49	12	12	0.78	0.83	0.11	0.03%		34	10	10	1.00	0.86	0.74	0.04%	
D22	49	11	12	0.76	0.86	0.01	0.01%		34	12	12	0.85	0.88	0.87	0.02%	
Dde59	49	14	14	0.92	0.91	0.42	0.04%		34	14	40	0.79	0.87	0.62	0.03%	
Dde65	49	7	10	0.69	0.72	0.38	0.04%		34	6	10	0.71	0.75	0.53	0.04%	
Dde66	48	12	18	0.63	0.71	0.15	0.02%		34	10	16	0.94	0.81	0.74	0.04%	
Dde69	49	15	18	0.92	0.89	0.02	0.01%		34	8	16	0.88	0.85	0.89	0.03%	
Dde70	49	12	23	0.82	0.82	0.72	0.03%		34	9	17	0.62	0.72	0.26	0.04%	
Dde72	49	18	35	0.92	0.93	0.06	0.01%		34	18	28	0.94	0.91	0.89	0.03%	
Dde84	49	8	8	0.71	0.71	0.89	0.02%		34	8	9	0.62	0.65	0.54	0.05%	
EV37	49	9	8	0.78	0.80	0.43	0.03%		34	10	11	0.76	0.74	0.58	0.04%	
KWM2b	49	6	6	0.59	0.71	0.08	0.02%		34	5	5	0.56	0.69	0.54	0.05%	
KWM9b	49	7	6	0.65	0.70	0.65	0.04%		34	9	11	0.79	0.78	0.88	0.03%	
MK3	49	6	5	0.78	0.80	0.54	0.05%		34	8	7	0.79	0.78	0.34	0.04%	
MK5	49	12	15	0.57	0.65	0.06	0.02%		34	9	16	0.56	0.60	0.30	0.04%	
Sco11	49	6	12	0.78	0.81	0.69	0.06%		34	6	12	0.85	0.82	0.92	0.03%	
Sco28	49	4	9	0.14	0.14	1.00	0.00%		34	3	6	0.12	0.11	1.00	0.00%	
Sco55	49	4	3	0.49	0.44	1.00	0.00%		34	4	3	0.47	0.49	0.44	0.05%	
Mean		9.278	12.389	0.68	0.70					8.556	13.278	0.70	0.70			
s.d.		4.142	7.625	0.21	0.22					3.666	8.737	0.23	0.21			

Table A.2 shows high genetic diversity for Risso's dolphins across the studied region, and no significant indication of expansion based on Tajima's D or Fu's Fs estimates. Table A.4 shows pairwise comparisons for F_{ST} , θ_{ST} and R_{ST} for mtDNA and microsatellite data. The NEP population shows consistent significant differentiation from all other populations, while WTP (Taiwan & the Philippines) and NWP (Japan) were significantly differentiated only for mtDNA based on F_{ST} . This pattern is consistent with the results from the factorial correspondence analysis (FCA; Figure A.2). The Structure analysis suggested a two population model for our study (for both $\ln PK$ and ΔK ; Figure A.3), again highlighting the differentiation of the NEP population.

Table A.4: Pairwise population comparison. *: $P < 0.05$; **: $P < 0.01$

		MtDNA control region (473bp)				18 microsatellite loci			
		θ_{ST}^1				R_{ST}			
Location	n	ETP	NEP	NWP	WTP	ETP	NEP	NWP	WTP
		21	23	50	42	23	77	34	49
F_{ST}	ETP		0.024	0.088**	0.123**		0.009	-0.003	-0.005
	NEP	0.039*		0.033	0.078*	0.015**		0.013*	0.023**
	NWP	0.084**	0.045**		-0.001	0.006	0.010**		0.007
	WTP	0.114**	0.066**	0.023*		0.009**	0.016**	0.002	

1: Tamura & Nei model

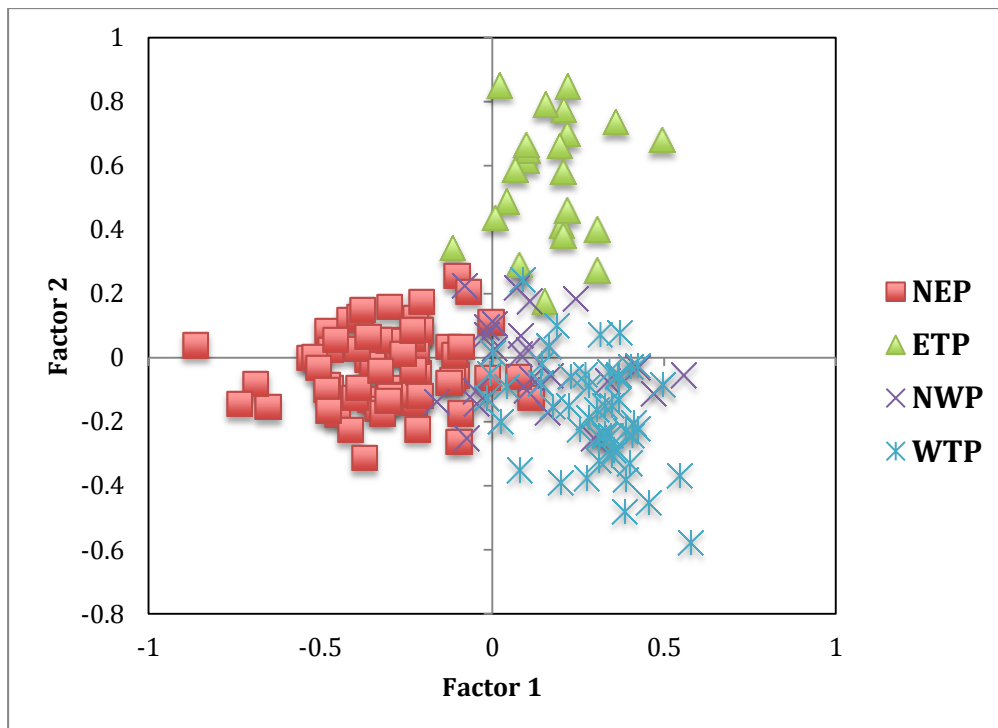


Figure A.2: Result from Factorial Correspondence analysis (18 microsatellite loci).

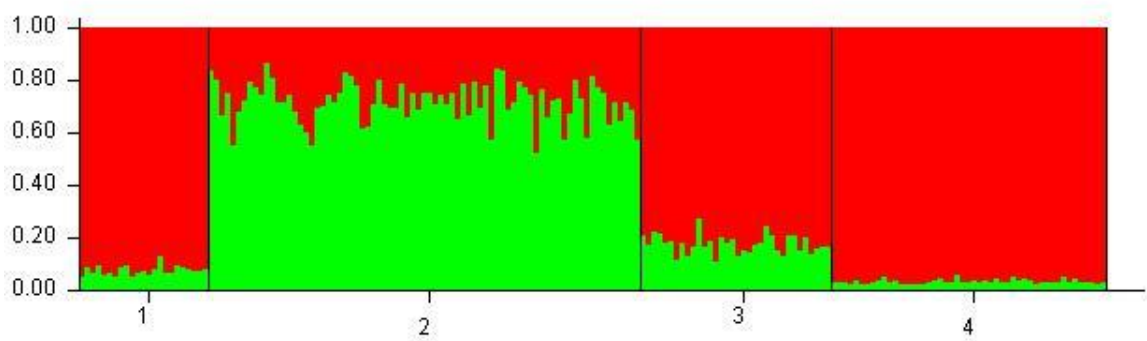


Figure A.3: Structure analysis for K=2. Labels for populations: 1- ETP; 2- NEP; 3- NWP; 4- WTP.

Further analyses of demographic parameters based on coalescent analyses will be presented in the final report.

Section B. Fraser's dolphins

Table B.1 and Figure B.1 showed the numbers and origins of Fraser's dolphin samples acquired for this project. The total number of specimens sampled was 111, and most of the samples were collected from Taiwanese and Philippine waters. The samples for Northwest Pacific (NWP) were from a school of dolphins culled in a single whaling event in Japan in 1991. Microsatellite data for 105 samples are presented here.

Table B.1: Numbers and origins of the samples. See Figure B.1 for location definition.

Location	Sampling period	n [#]	n by sampling methods			
			Biopsy	Stranding	Bycatch	Direct catch
NWP	1991	37 (36)				37
WTP-N	1994-2013	46 (45)		22	24	
WTP-S	1991-1997	24 (20)			21	
ETP	1975-2002	4 (4)	3		1	

#: Number in parentheses indicates the n being used in the analysis below.

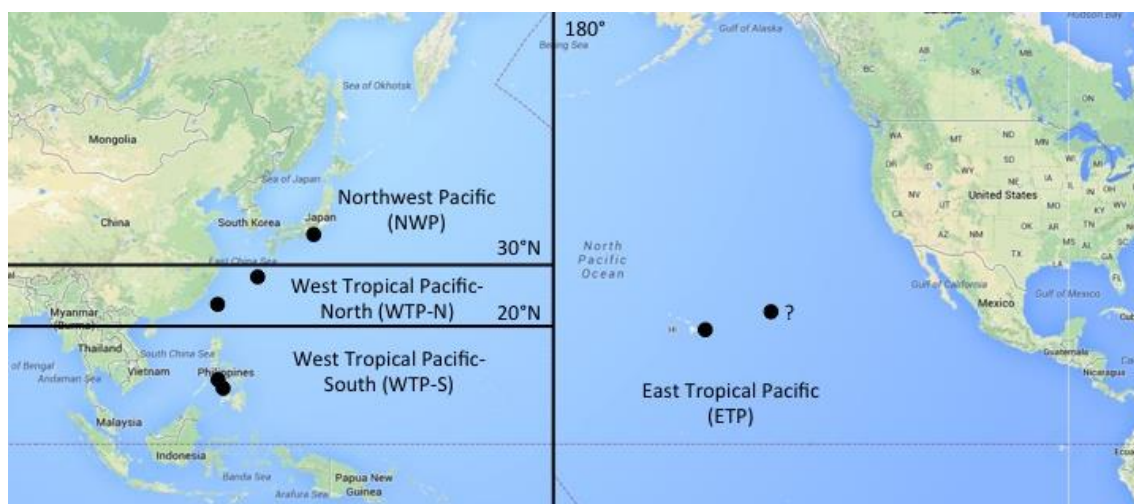


Figure B.1: Map indicates the approximate sampling locations. Samples were assigned into four groups by geographic features, Northwest Pacific (NWP), West Tropical Pacific-North (WTP-N), West Tropical Pacific-South (WTP-S) and East Tropical Pacific (ETP) by 20°N, 30°N and 180°. See Table B.1 for the number of samples from each location.

For the analysis we used 17 microsatellite loci (Table B.2). Deviation from Hardy-Weinberg Equilibrium was detected in multiple loci in different populations (Table B.2), but especially in the WTP-N population. All loci are retained for the analyses presented here, while data based on a subset of loci will be presented in the final report. The higher level of HWE deviation in WTP-N may reflect mixing and a Wahlund effect (see below).

Table B.2. Microsatellite allele numbers, allele range, Observed and expected heterozygosity and Hardy-Weinberg Equilibrium test results. Loci in red show significant HWE deviation at the $p < 0.05$ level (blue after Bonferroni correction).

Location	WTP-S							WTP-N						
	#Genot	#alleles	Allelic range	Obs.Het.	Exp.Het.	P-value	s.d.	#Genot	#alleles	Allelic range	Obs.Het.	Exp.Het.	P-value	s.d.
AAT44	19	7	10.00	0.842	0.819	0.578	0.05%	45	11	11.00	0.689	0.809	0.040	0.01%
D14	20	6	7.00	0.750	0.776	0.479	0.04%	45	8	9.00	0.733	0.746	0.332	0.05%
D22	20	3	4.00	0.200	0.188	1.000	0.00%	45	3	4.00	0.467	0.481	0.655	0.05%
Dde65	20	7	14.00	0.900	0.801	0.418	0.05%	45	10	18.00	0.689	0.759	0.011	0.01%
Dde69	20	4	6.00	0.550	0.622	0.364	0.05%	45	9	12.00	0.578	0.762	0.000	0.00%
Dde70	20	4	6.00	0.750	0.604	0.284	0.05%	44	8	9.00	0.432	0.595	0.033	0.02%
Dde72	20	8	11.00	0.900	0.791	0.522	0.04%	45	10	13.00	0.800	0.799	0.700	0.04%
Dde84	20	6	10.00	0.800	0.850	0.688	0.04%	44	9	11.00	0.636	0.806	0.000	0.00%
KWM1b	17	4	4.00	0.765	0.578	0.059	0.02%	45	8	8.00	0.533	0.629	0.042	0.02%
KWM2b	19	4	7.00	0.211	0.289	0.034	0.02%	44	7	11.00	0.318	0.668	0.000	0.00%
KWM9b	19	8	10.00	0.737	0.787	0.545	0.03%	45	8	16.00	0.578	0.784	0.025	0.01%
MK3	18	8	11.00	0.944	0.857	0.613	0.05%	44	16	18.00	0.773	0.861	0.004	0.00%
MK5	20	8	13.00	1.000	0.853	0.116	0.03%	45	11	15.00	0.800	0.832	0.289	0.03%
Sco11	Monomorphic locus							Monomorphic locus						
Sco28	20	2	2.00	0.450	0.409	1.000	0.00%	45	2	2.00	0.378	0.362	1.000	0.00%
Sco55	20	2	1.00	0.050	0.050	1.000	0.00%	45	2	1.00	0.067	0.065	1.000	0.00%
TexVet7	20	4	11.00	0.650	0.619	0.456	0.05%	44	7	13.00	0.705	0.665	0.495	0.05%
Mean	19.50	5.31	7.94	0.656	0.618			44.69	8.06	10.69	0.573	0.664		
s.d.	0.89	2.18	3.89	0.287	0.256			0.48	3.57	5.12	0.202	0.209		

Location	ETP							NWP						
	#Genot	#alleles	Allelic range	Obs.Het.	Exp.Het.	P-value	s.d.	#Genot	#alleles	Allelic range	Obs.Het.	Exp.Het.	P-value	s.d.
AAT44	4	4	4.00	1.000	0.750	1.000	0.00%	35	11	16.00	0.600	0.757	0.001	0.00%
D14	4	4	9.00	0.750	0.643	1.000	0.00%	36	10	12.00	0.778	0.774	0.652	0.04%
D22	Monomorphic locus							36	3	4.00	0.361	0.356	0.650	0.05%
Dde65	4	5	10.00	0.750	0.857	0.654	0.05%	36	7	14.00	0.722	0.716	0.612	0.05%
Dde69	4	3	6.00	0.750	0.714	1.000	0.00%	36	5	8.00	0.583	0.635	0.029	0.02%
Dde70	4	4	6.00	0.500	0.786	0.317	0.05%	36	4	3.00	0.556	0.452	0.646	0.05%
Dde72	4	5	13.00	1.000	0.786	1.000	0.00%	36	11	15.00	0.833	0.878	0.073	0.03%
Dde84	4	5	4.00	0.750	0.857	0.658	0.06%	36	6	10.00	0.778	0.773	0.901	0.03%
KWM1b	4	3	2.00	0.750	0.679	1.000	0.00%	36	4	4.00	0.778	0.628	0.330	0.05%
KWM2b	4	4	7.00	0.750	0.750	0.312	0.05%	36	4	7.00	0.389	0.433	0.528	0.05%
KWM9b	4	3	4.00	0.750	0.679	1.000	0.00%	36	10	17.00	0.778	0.784	0.165	0.03%
MK3	4	5	8.00	1.000	0.857	1.000	0.00%	36	10	11.00	0.833	0.801	0.561	0.05%
MK5	4	5	12.00	1.000	0.893	1.000	0.00%	36	12	23.00	0.806	0.850	0.440	0.04%
Sco11	Monomorphic locus							36	2	14.00	0.056	0.055	1.000	0.00%
Sco28	Monomorphic locus							36	2	2.00	0.500	0.380	0.078	0.03%
Sco55	Monomorphic locus							36	2	1.00	0.111	0.106	1.000	0.00%
TexVet7	4	4	11.00	0.750	0.821	0.314	0.04%	36	7	12.00	0.667	0.749	0.200	0.04%
Mean	4.00	4.15	7.38	0.808	0.775			35.94	6.47	10.18	0.596	0.596		
s.d.	0.00	0.80	3.45	0.150	0.080			0.24	3.56	6.12	0.243	0.254		

Table B.3 shows the pairwise comparisons for F_{ST} and R_{ST} . The NWP population appeared to be the most distinct but these samples were all collected from the same school of dolphins and the result might be influenced by kinship (to be assessed). Figure A. 2 shows the FCA plot, which suggests three populations, though it is not clear if a larger sample from ETP may show a distinct cluster. Figure A.3 shows the analysis from Structure, indicating three populations (for both InPK and ΔK) and suggests mixing in the WTP-N sample, consistent with the HWE deviation results.

Table B.3: Pairwise population comparison for populations with 20 or more samples (17 microsatellite loci, including loci that did not pass HWE test) *: $P < 0.05$; **: $P < 0.01$.

	Location	R_{ST}		
		WTP-S	WTP-N	NWP
		20	45	36
F_{ST}	WTP-S		0.014	0.024*
	WTP-N	0.010*		0.003
	NWP	0.024**	0.021**	

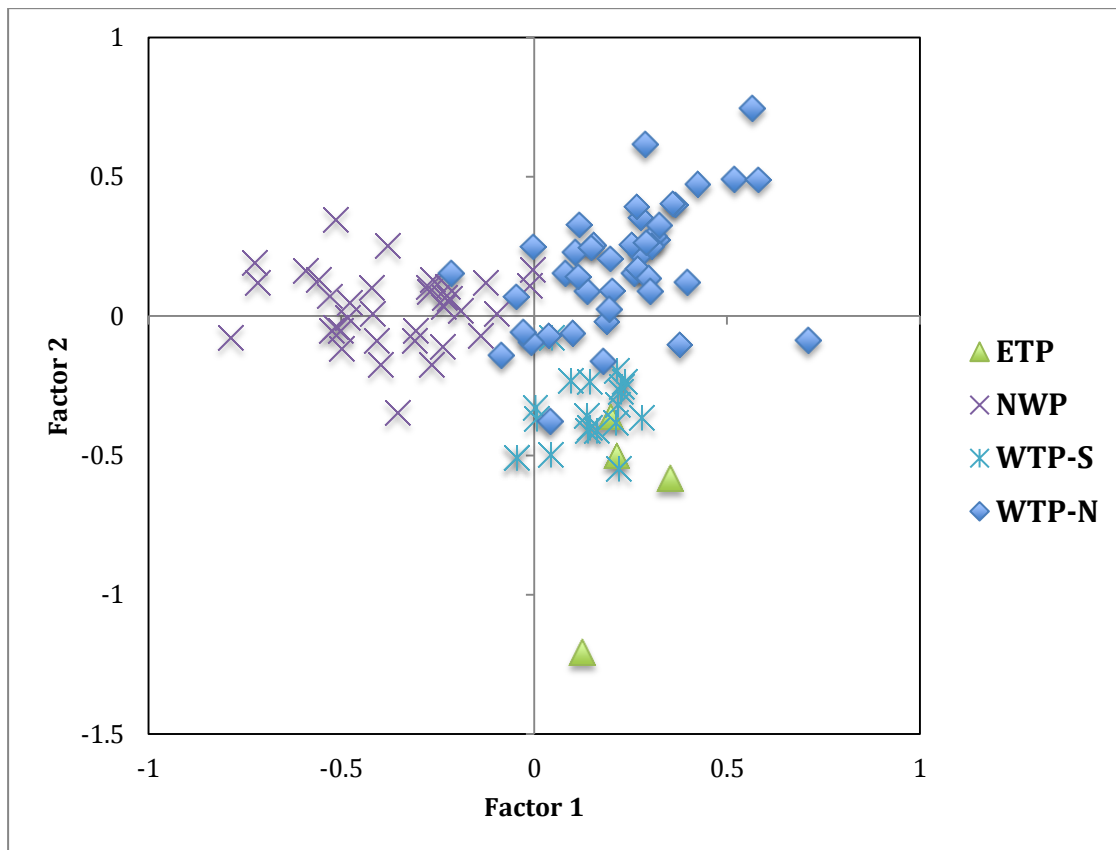


Figure B.2: Result from Factor Correspondence analysis (17 microsatellite loci).

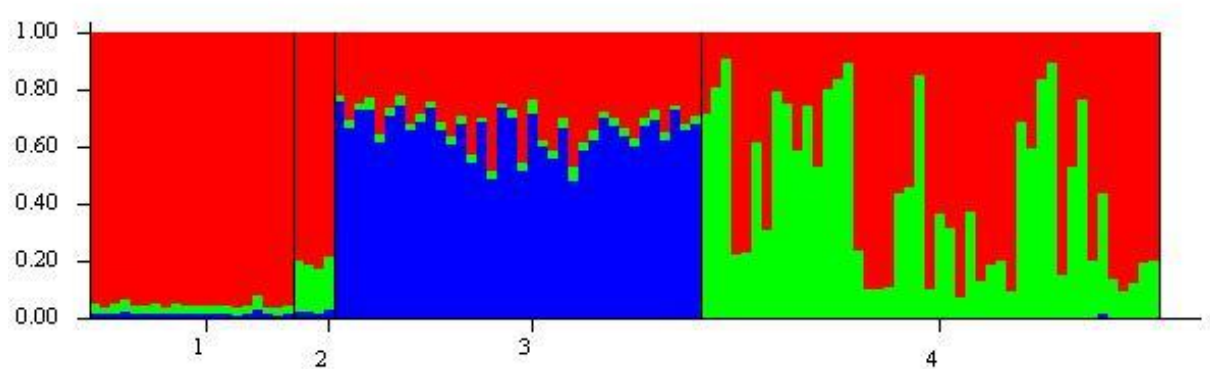


Figure B.3: Structure analysis K=3 (determined by Structure Harvester). Labels for populations: 1 - WTP-S; 2 - ETP; 3 - NWP; 4 - WTP-N.

Section C. 'Pingdong' dolphin identification

On 5 May 2005, the Taiwanese authority confiscated about 1,000 kg of dolphin meat from a garage which provided freezing service in Tunggang, Pingdong, a harbour famous for its offshore fisheries in southern Taiwan (Figure C.1). The dolphins had been cut into pieces, but 10 were identified as Fraser's dolphins, possibly based on their external characters (i.e., colour pattern, see example in Figure C.2).



Figure C.1. The confiscation. Photograph copyright: Taiwan Cetacean Society.



Figure C.2. One of the 10 dolphins that were identified as Fraser's dolphin in the species identification report composed by Taiwan Cetacean Society and submitted to Pingdong County Council. Photograph copyright: Taiwan Cetacean Society.

Here we present preliminary data from three genetic markers, the mtDNA cytochrome b gene (cytb, 798bp), mtDNA control region (505bp) and the DBY gene on the Y chromosome (251bp), to assess species identity for these dolphins (Figure C.3, C.4 and C.5). All trees were constructed in Mr. Bayes using the GTR + g model, and run for at least 20,000 generations. The outgroup for all trees was *Sousa chinensis*. Although the control region sequence showed no consistent clustering, both cytb and the DBY7 were more consistent with a match to a species in the genus *Stenella*, especially spinner dolphin (*S. longirostris*). Clustering with clymene dolphin (*S. clymene*) for cytb may be consistent with the suggestion of hybrid origin for this species (Amaral et al. 2014), where *S. clymene* is shown to share haplotypes with *S. longirostris*. We will be incorporating further taxa and loci and considering partitioning and congruence models to try to resolve this further, as the present trees clearly present issues with taxon sampling and polyphyly. Unusual pigmentation patterns together with the genetic data suggest the possibility of hybridisation, which will be explored further.

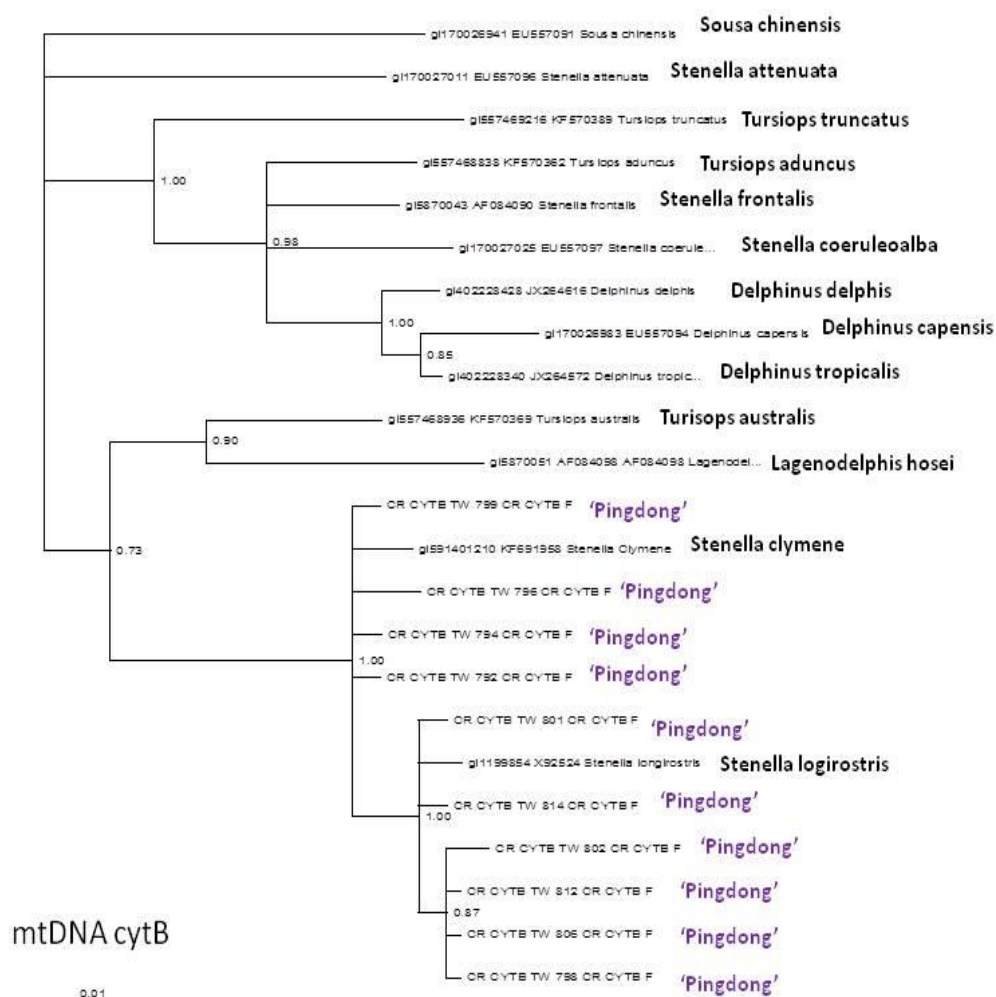


Figure C.3: Phylogenetic relationship of the 'pingdong dolphins' according to mtDNA cytochrome b gene (798bp).

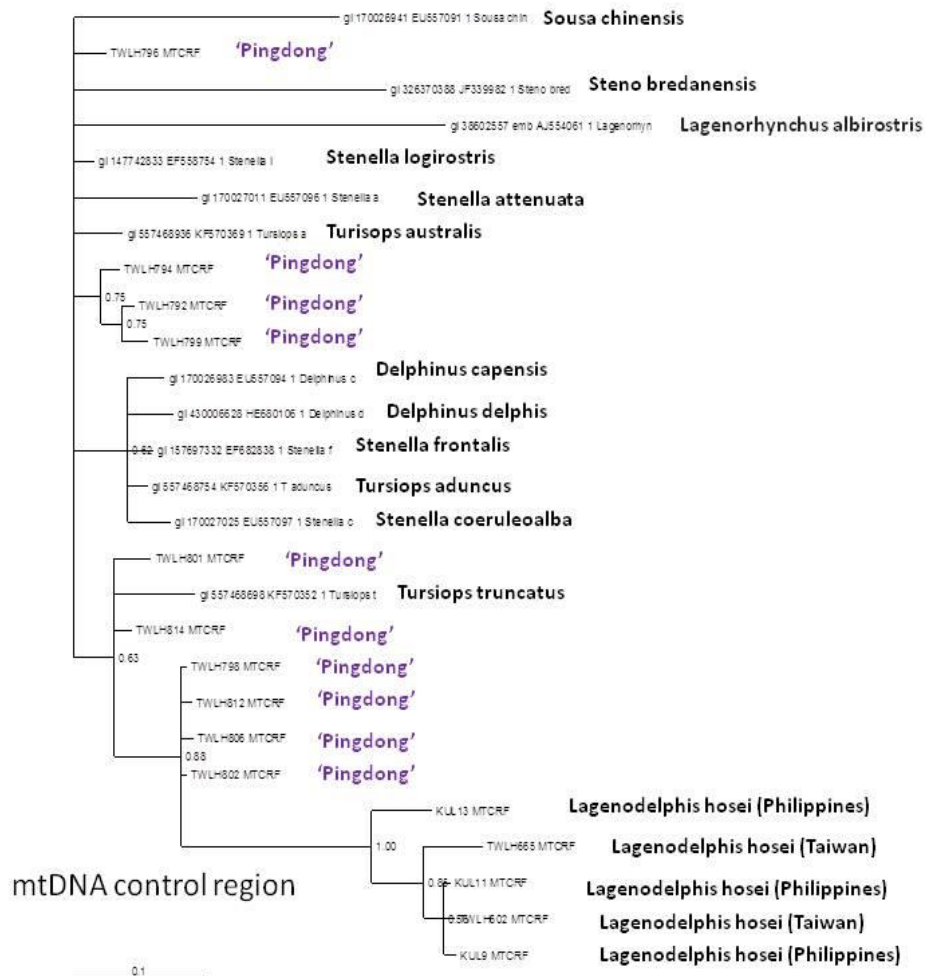


Figure C.4: Phylogenetic relationship of the 'pingdong dolphins' reconstructed by mtDNA control region sequences (505bp).

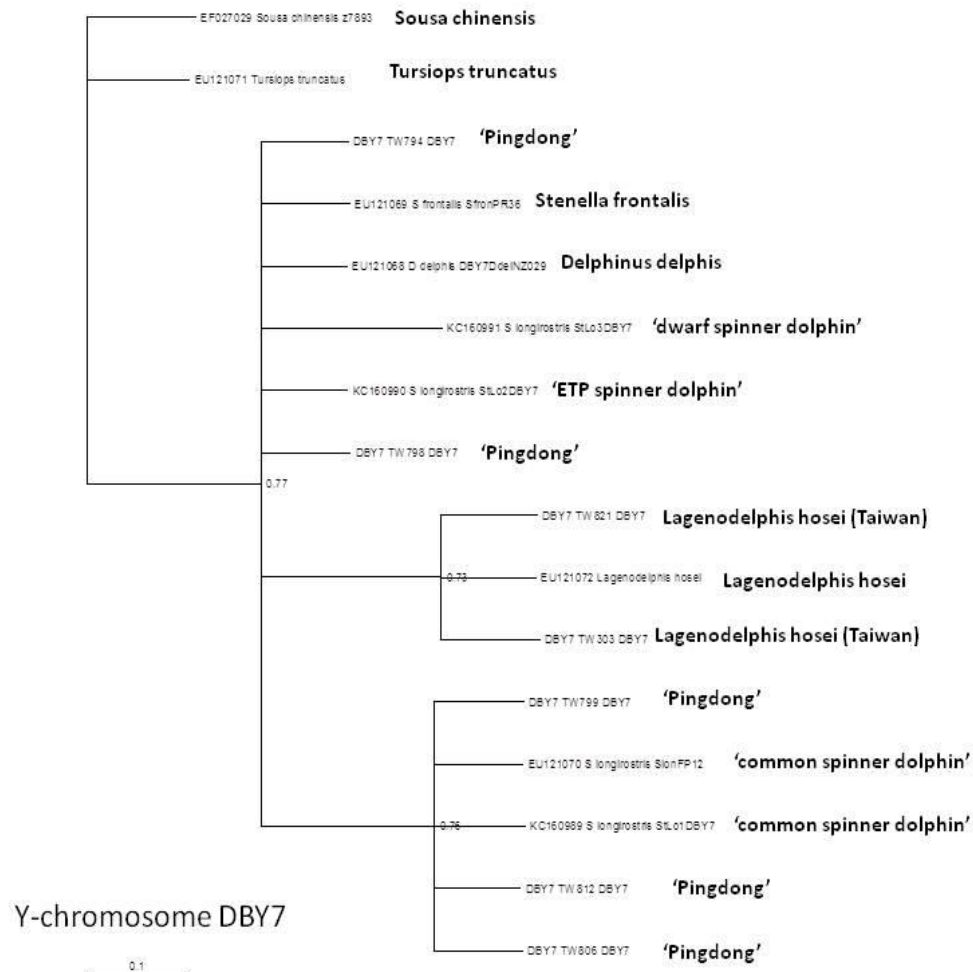


Figure C.5: Phylogenetic relationship of the 'pingdong dolphins' reconstructed by a male specific DBY gene (251bp).

Section D. Public engagement

Preliminary results from this project have been presented at three international and regional conferences: the Annual Taiwan Fishery Society Meeting (Chiayi, Taiwan, 8 January 2014), the Congress of Animal Behavior and Ecology 2014 (Taichung, Taiwan, 20-21 January 2014) and the 28th European Cetacean Society Annual Meeting (Liege, Belgium, 5-9 April 2014). The result will also be presented at the Japanese Cetacean Research Group Meeting in Matsuyama, Japan in May 2014. A final report will be written for the Taiwanese authorities to provide scientific background knowledge and encourage conservation management.

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