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Population genetic diversity and historical dynamics of Fraser's dolphins *Lagenodelphis hosei*

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ABSTRACT: Marine organisms face relatively few barriers to gene flow, and yet even highly mobile species such as dolphins often show population structure over regional geographic scales. Understanding the processes that promote this pattern of differentiation helps us understand the evolutionary radiation of this group, and to promote more effective measures for conservation. Here we report the first population genetic study of Fraser's dolphin *Lagenodelphis hosei* (Fraser, 1956), a species that was not recognized by the scientific communities until the early 1970s. We use 18 microsatellite DNA loci and 1 mitochondrial DNA (mtDNA) locus to compare 112 Fraser's dolphins collected in various locations, mainly from the waters off Japan, Taiwan, and the Philippines, but also including samples from the Gulf of Mexico and Caribbean Sea. Our results indicate differentiation between populations in waters off Japan, Taiwan, and the Philippines, and support the findings from earlier morphological assessments for differentiation between Japanese and Philippine waters. Small sample sets also show likely differentiation between other regions in the North Pacific and North Atlantic Oceans. Moreover, neutrality tests and mismatch analysis based on mtDNA data indicate that the populations in the western North Pacific Ocean have expanded demographically and spatially, possibly since the latest global deglaciation, when sea levels and global temperatures started to rise.

KEY WORDS: Population structure · Marine mammal · Northwest Pacific Ocean · Conservation · Climate change

1. INTRODUCTION

Understanding population structure is essential for establishing useful inferences about the process of local adaptation and evolution (Kawecki & Ebert 2004), as well as for developing conservation strategies in natural resource management (Palsbøll et al. 2007). Assessing population structure for oceanic cetaceans (whales, dolphins, and porpoises) can be particularly challenging, not only because their highly dynamic open water environment usually offers little clue about potential population boundaries, but

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also because the population structure is often shaped in various contexts by multiple intrinsic biological factors, such as resource exploitation, physiological constraints, or behavioural/cultural stereotyping (e.g. Hoelzel 2018).

On the other hand, environmental factors such as climate change can also play a significant role in shaping marine biodiversity patterns at both regional and global scales (Renema et al. 2008, Cheung et al. 2009). It has been proposed that past climate oscillations have influenced the distributions of many contemporary cetacean species or populations, particularly for those living in middle to higher latitude waters (e.g. Hayano et al. 2004, Harlin-Cognato et al. 2007, Pastene et al. 2007, Banguera-Hinestroza et al. 2010, 2014, Taguchi et al. 2010, Amaral et al. 2012, Moura et al. 2013). However, little is reported for species from tropical waters. As modelling analyses have shown that the current global warming phenomenon could affect marine mammal diversity and distribution range globally (MacLeod 2009, Kaschner et al. 2011), further information regarding the population structure of tropical species is needed.

Fraser's dolphin *Lagenodelphis hosei* is one of the least studied dolphin species in the world. The species was unknown to the scientific community until Fraser (1956) described a specimen collected in 1895 from Sarawak, Borneo. Yet, the existence of any living Fraser's dolphins was not confirmed until the early 1970s, when further fresh specimens from the Eastern Tropical Pacific (ETP), South Africa, Australia, Taiwan, and Japan, as well as sighting records of living individuals in the ETP and Central North Pacific (CNP), started to emerge (Perrin et al. 1973, Tobayama et al. 1973). Further sightings, strandings, and bycatch records from the North and South Atlantic Ocean were reported in subsequent decades (Caldwell et al. 1976, Hersh & Odell 1986, Leatherwood et al. 1993, Bones et al. 1998, Mignucci-Giannoni et al. 1999, Moreno et al. 2003, Weir et al. 2008, Gomes-Pereira et al. 2013). Fraser's dolphins are widespread in pan-tropical regions of the Pacific, Atlantic, and Indian Oceans, and their presence is usually associated with a particular combination of environmental characteristics, including deep water with tropical or subtropical climate (Hammond et al. 2012, Jefferson et al. 2015, Dolar 2018). This species has been proposed to be a possible marine bio-indicator of climate change, as its recent range expansion in the North Atlantic appears to reflect the increase in regional seawater temperatures in the temperate waters of the Azores (Gomes-Pereira et al. 2013).

Geographic variation for the species has been reported for pigmentation patterns (e.g. between dolphins from South Africa and the ETP; Perrin et al. 1973), body size (dolphins found off France seem to be larger than those found in the western North Pacific, Van Bree et al. 1986; however, this observation was later questioned by Amano et al. 1996), skull morphometric measurements (relatively larger and broader skulls for dolphins in Japanese waters than in Philippine waters; Perrin et al. 2003), and social assemblages (smaller pod size in the North Atlantic than in the North Pacific; Gomes-Pereira et al. 2013). However, morphological and behavioural characteristics can be plastic, and may not always reflect the pattern of gene flow (West-Eberhard 1989, Crispo 2008, Prada et al. 2008). Small sample size and sampling area coverage was also a limitation for some of these earlier studies.

Here, we assess the genetic diversity and population structure of Fraser's dolphins, with a focus on the East Asian regions, where this species is considered to have been negatively affected by fisheries activities (e.g. frequent involvement in incidental or direct catches; Jefferson & Leatherwood 1994, Perrin et al. 2005, Porter & Lai 2017, Altherr & Hodgins 2018). Based on the conclusions of an earlier morphological study (Perrin et al. 2003), we hypothesized that Fraser's dolphin populations would be genetically differentiated between the Pacific and Atlantic Oceans, and between Japanese and Philippine waters. We also tested the hypothesis that coincident with past periods of global warming including the last deglaciation, we may find evidence for population expansion associated with population growth in Fraser's dolphins, consistent with that proposed for other tropical species (MacLeod 2009, Gomes-Pereira et al. 2013).

2. MATERIALS AND METHODS

2.1. Sample collection, DNA fragment amplification, and genotyping

The 112 samples used in this study were collected from dead Fraser's dolphins that either beach-casted or had perished in fishery interactions, except for 3 samples from the CNP, which were biopsied from free-ranging dolphins (Table S1 in Supplement 1, www.int-res.com/articles/suppl/m643p183_supp1.xlsx). Based on sampling localities, we categorized the samples into 7 geographic groups: Japan, Taiwan, the Philippines, CNP, ETP, Gulf of Mexico (GM), and

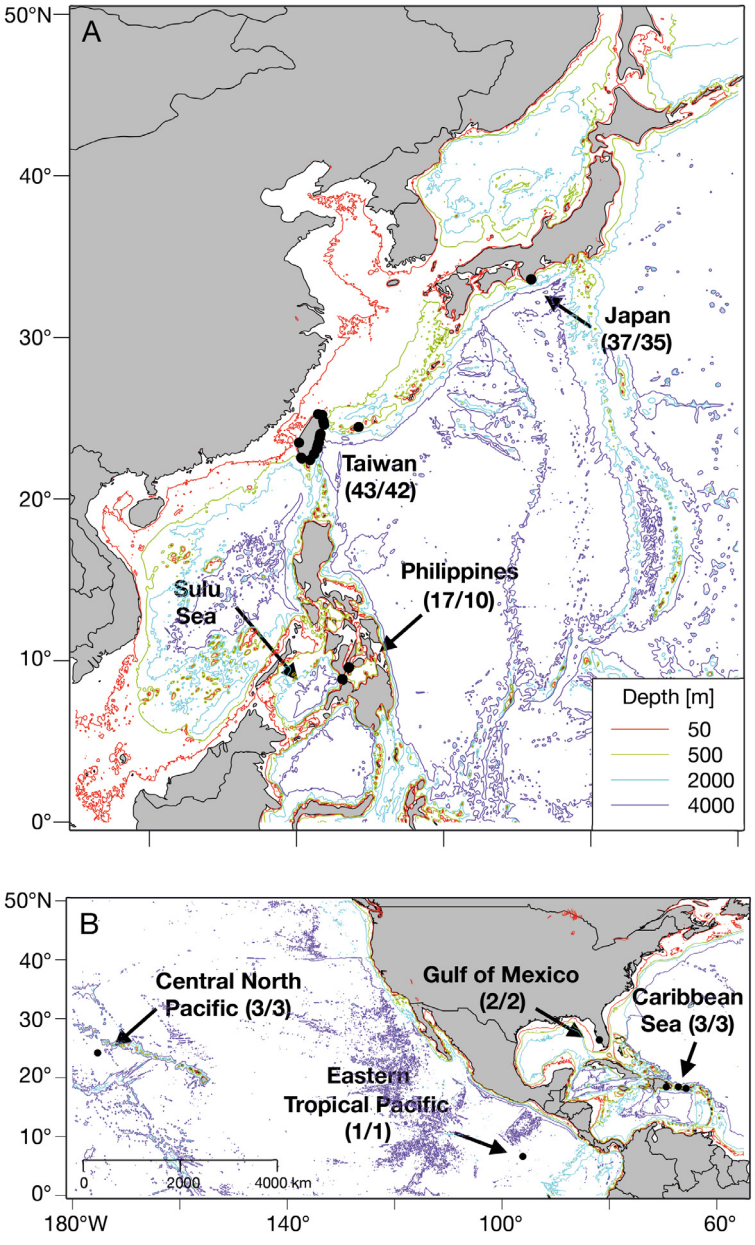

Fig. 1. Sampling locations for Fraser's dolphins in (A) Asia and (B) Pacific and Caribbean regions. Black dots indicate sampling locations, and the numbers in parentheses indicate the sample size used in microsatellite/mitochondrial DNA analyses

the Caribbean Sea (CS) (Fig. 1). The species and sex identity was acquired from the archive records where the identification was based on the external morphological characters of the specimens. When in doubt, this was verified by our genetic assessments. Samples supplied by the Southwest Fisheries Science Center (USA) were titrated DNA solutions; otherwise, samples were provided as a small portion of skin or muscle tissue samples preserved in either 99% ethanol or 20% DMSO solution saturated with sodium chloride. All specimens, except the 3 Philippine specimens archived in es-BANK (Ehime University, Japan), were transported to, and examined in, the Molecular Ecology Group Laboratory at Durham University, with valid official permits issued by the authorities of Japan, Taiwan, the USA, and the UK.

The genomic DNA of tissue samples was isolated and purified using a standard Proteinase K digestion/phenol–chloroform extraction protocol (Sambrook et al. 1989). We examined 18 microsatellite loci (AAT44, D14, D22, KWM1b, KWM2b, KWM9b, TexVet5, TexVet7, MK3, MK5, Dde65, Dde69, Dde70, Dde72, Dde84, Sco11, Sco28, and Sco55; see Table S2) and 1 mitochondrial DNA (mtDNA) locus (779 bp of the control region using the primers described by Hoelzel et al. 1991) that have been used in earlier population genetic studies for other delphinid species, following the same procedure as described by Chen et al. (2017). Briefly, annealing was at 40°C (for mtDNA) and the amplification ran for 35 cycles, with the purified product sequenced on an ABI 3730 in the forward direction. The optimal annealing temperatures and allele size ranges of each microsatellite locus are provided in Table S2.

2.2. Microsatellite data analysis

Micro-Checker 2.2.3 (Van Oosterhout et al. 2004) was used to screen for null alleles and potential scoring errors. The R package 'pegas' (Paradis 2010) was used to estimate observed heterozygosity (H_o) and expected heterozygosity (H_e), and to test for Hardy-Weinberg equilibrium (HWE) for the sampled loci. The number of replicates for the Monte Carlo procedure was set to the default value (B = 1000). A locus was assessed for deviation from HWE using both the χ^2 test and the exact test based on Monte Carlo permutations of alleles, and excluded from further analyses if $p < 0.001$. The inbreeding coefficient (F) was estimated for each individual using the 'inbreeding' function implemented in the R package 'adegenet' (Jombart 2008). Because the Japanese sample was from a single sampling event, we ran a kinship analy-

sis using the program 'Kingroup' (Konovalov et al. 2004) including only individuals from the Japanese sample set.

The degree of population differentiation among the geographic groups was evaluated through *F*-statistics, and the significance was tested using *G*-statistic tests (Goudet et al. 1996), using functions implemented in 'hierfstat' (Goudet 2005) and 'pegas', with the number of simulations set to 1000. Pairwise F_{ST} values (Nei 1987) among the 3 major sampling groups (i.e. the Philippines, Taiwan, and Japan) were calculated using 'hierfstat'. A 95% confidence interval (CI) was generated with 1000-fold bootstrap resampling. The discriminant analysis of principal components (DAPC, Jombart et al. 2010) implemented in 'adegenet' was also used to assess genetic structure and interpret individual membership. Fifteen principal components (determined according to the *a*-score analysis; Jombart et al. 2010) and 100 discriminant analysis steps were retained in the analysis. Factorial correspondence analysis (FCA) implemented in Genetix 4.0 (Belkhir et al. 2004) was applied as a complementary ordination analysis. We used the 'sur population' option, since the aim was to reveal differentiation among geographic groups rather than among individuals.

Spatial population genetic structure was assessed using 'Geneland' (Guillot et al. 2005). The data were analysed using the correlated allele frequency model and the spatial model; the uncertainty associated with the spatial coordinates was set as 1 decimal place, the maximum rate of Poisson process was fixed to 100, and the maximum number of nuclei in the Poisson-Voronoi tessellation was fixed to 300. The number of Markov chain Monte Carlo (MCMC) iterations was set to 10^6, with a thinning at every 1000 iterations, and K was set to vary from 1 to 10. To construct the population distribution map, we set the burn-in to 200 iterations, and the spatial domain to 174 pixels along the *x*-axis and 27 along the *y*-axis. We also used the Mantel test implemented in 'adegenet' to test the effect of isolation by distance (IBD), using both Nei's distance (non-Euclidean) and Edwards' distance (Euclidean) to estimate genetic distance, and the Euclidean distance for geographic distance at the population level.

2.3. Mitochondrial DNA analysis

The mtDNA sequences were aligned and assessed using MEGA 5.05 (Tamura et al. 2011). A median-joining network was constructed using PopART (Bandelt et al. 1999, Leigh & Bryant 2015). Gene diversity (h), nucleotide diversity (π), Tajima's D, and Fu's Fs were estimated using DnaSP 5.10 (Librado & Rozas 2009). Historic demographic or spatial expansion was evaluated using the analysis of mismatch distributions implemented in Arlequin 3.5 (Excoffier & Lischer 2010). This was done for each putative population on its own, and for all western North Pacific samples (i.e. Japan, Taiwan, and the Philippines) combined as 1 population. The CI for the mismatch estimates was obtained from 10^4 bootstrap simulations of an instantaneous expansion under a coalescent framework. Model fit was evaluated according to the significance of the sum of square deviations (SSD) between the observed and the expected mismatch and the raggedness index (r) of the observed distribution (Harpending 1994, Schneider & Excoffier 1999).

An approximate time of expansion (T) was calculated through the formula $T = \tau/2u$, where τ is the simulated time of demographic or spatial expansion estimated in the mismatch analysis, and u is the mutation rate for the sequence in use (per locus per generation; Rogers 1995). We used an estimated generation time of 11.1 yr (Taylor et al. 2007), and used 2 substitution rate values: 1×10^{-7} substitutions site^{-1} yr^{-1} (Ho et al. 2011) and 7×10^{-8} substitutions site^{-1} yr^{-1} (Harlin et al. 2003).

Arlequin was used to estimate pairwise F_{ST} and Φ_{ST}. We used the Tamura Nei model to estimate Φ_{ST} because it was the closest model available to the TVM+I model, which was suggested as the best model for our samples according to the result of Akaike's information criterion (AIC) in 'jModelTest' 2.1.6 (Darriba et al. 2012). The level of differentiation between sample group pairs was estimated with 10^4 permutations.

3. RESULTS

3.1. Microsatellite data analysis: genetic diversity

Useful microsatellite data were obtained from 106 samples (Fig. 1; Table S1). Nine samples had missing data at 1–4 loci (not shown). The 18 loci examined were all polymorphic, with the number of alleles ranging from 2 to 17 (Table S3). None of these loci showed consistent deviation from HWE across the 3 major sampling groups (Japan, Taiwan, and the Philippines), so all were retained. However, for the Taiwan group, 5 loci showed signs of null alleles and deviations from HWE, although the magnitude of deviation

was always small. The reason for the larger proportion of loci out of HWE in Taiwan is not known, but given that the sample size was relatively large and collected over a relatively broad temporal period (see Table S1), a Wahlund effect is possible. Genotyping errors seemed less likely, due to the overall good quality of DNA and low divergence among populations. Deviation from HWE is expected due to the Wahlund effect when differentiated populations are combined, so the higher incidence of HWE deviation for combined datasets (Table S3) supports our interpretation of population structure (see Section 3.2). Mean H_o and H_e for the 3 major groups ranged from 0.54–0.62 and 0.57– 0.62, respectively (Table 1). The mean H_o was significantly lower than the mean H_e for the Taiwan group (upper-tailed paired *t*-test, t = 3.58, df = 17, p = 0.001). The Taiwan group also showed the highest average inbreeding coefficient (F = 0.21). The kinship analysis for the Japan group showed a mean pairwise kinship of r = −0.0277, implying that within-group kinship was unlikely to have affected our population-level analyses.

Table 1. Genetic variability of the 18 microsatellite loci examined in samples of Fraser's dolphins

Geographic group	n	Missing data rate (%)	No. of alleles	Mean H_e	Mean H_o	Mean F
Japan	37	0.15	115	0.6	0.61	0.165
Taiwan	43	0.78	137	0.62	0.54	0.214
Philippines	17	1.31	92	0.57	0.62	0.147
Central North Pacific (CNP)	3	0	52	0.59	0.59	
Gulf of Mexico (GM)	2	0	42	0.57	0.58	
Caribbean Sea (CS)	3	0	39	0.43	0.46	
Eastern Tropical Pacific (ETP)	1	0	30	NA	NA	
All samples	106	0.58		0.61	0.58	

Table 2. Pairwise genetic differences among the 3 main groups of Fraser's dolphins according to microsatellite data: above diagonal, F_{ST}; below diagonal, 95% confidence interval

	Japan	Taiwan	Philippines
Japan		0.0085	0.0133
Taiwan	0.003 – 0.015		0.0103
Philippines	0.005 – 0.021	−0.002 to 0.025	

3.2. Microsatellite data analysis: population structure

The *G*-statistic test result suggested the presence of population structure in our sample (p = 0.008; Fig. S1 in Supplement 2, www.int-res.com/articles/suppl/m643p183_supp2.pdf). Among the 3 groups with sufficiently large sample sizes, F_{ST} was most pronounced between the Philippines and Japan (F_{ST} = 0.013). Based on the 95% CI estimates, all pairwise F_{ST} values were significantly different from 0 except the Philippines–Taiwan pair (Table 2). For regions with small sample sizes, DAPC showed that the CS samples were most distinct (Fig. 2). The 3 major sampling groups (Japan, Taiwan, and the Philippines) could also be differentiated using both DAPC (Fig. 2) and FCA (Fig. S2) analyses. In the DAPC group membership assignment analysis, most individuals could be reassigned to their original clusters (including all groups with small sample sizes), although some potential admixture was found among all groups including Japan, Taiwan, and the Philippines (Fig. S3).

In the Geneland analysis, K = 4 was supported by the highest mean logarithm of posterior probability (Table S4) generating a population structure pattern (Fig. 3) broadly consistent with the pattern seen in our DAPC and FCA analyses (Fig. 2, Fig. S2). The Mantel test for IBD showed no significant effect of IBD in our sample, regardless of which method was used to estimate genetic distance (p = 0.948 with Nei's distance method; p = 0.897 with Edwards' distance method; Fig. S4).

3.3. Mitochondrial DNA data analysis

We amplified a 779 bp mtDNA control region sequence in 96 samples and identified 48 unique haplotypes characterized by 64 variable sites (Tables S1 & S5; the mtDNA sequences are available on GenBank, accession numbers MN268582–MN268677). The median-joining network showed little evidence of lineage sorting (Fig. 4). The number of haplotypes shared between Taiwan and Japan was more than that between Taiwan and the Philippines, or between the Philippines and Japan (Table S6).

The genetic and nucleotide diversity was high for Japan, Taiwan, and the Philippines (Table 3). All 3 groups had a negative Tajima's D, although none of the values were statistically different from 0. With the exception of the Philippines, all Fu's Fs estimates were also negative, and the values were statistically significant in Japan and Taiwan, indicating an excess

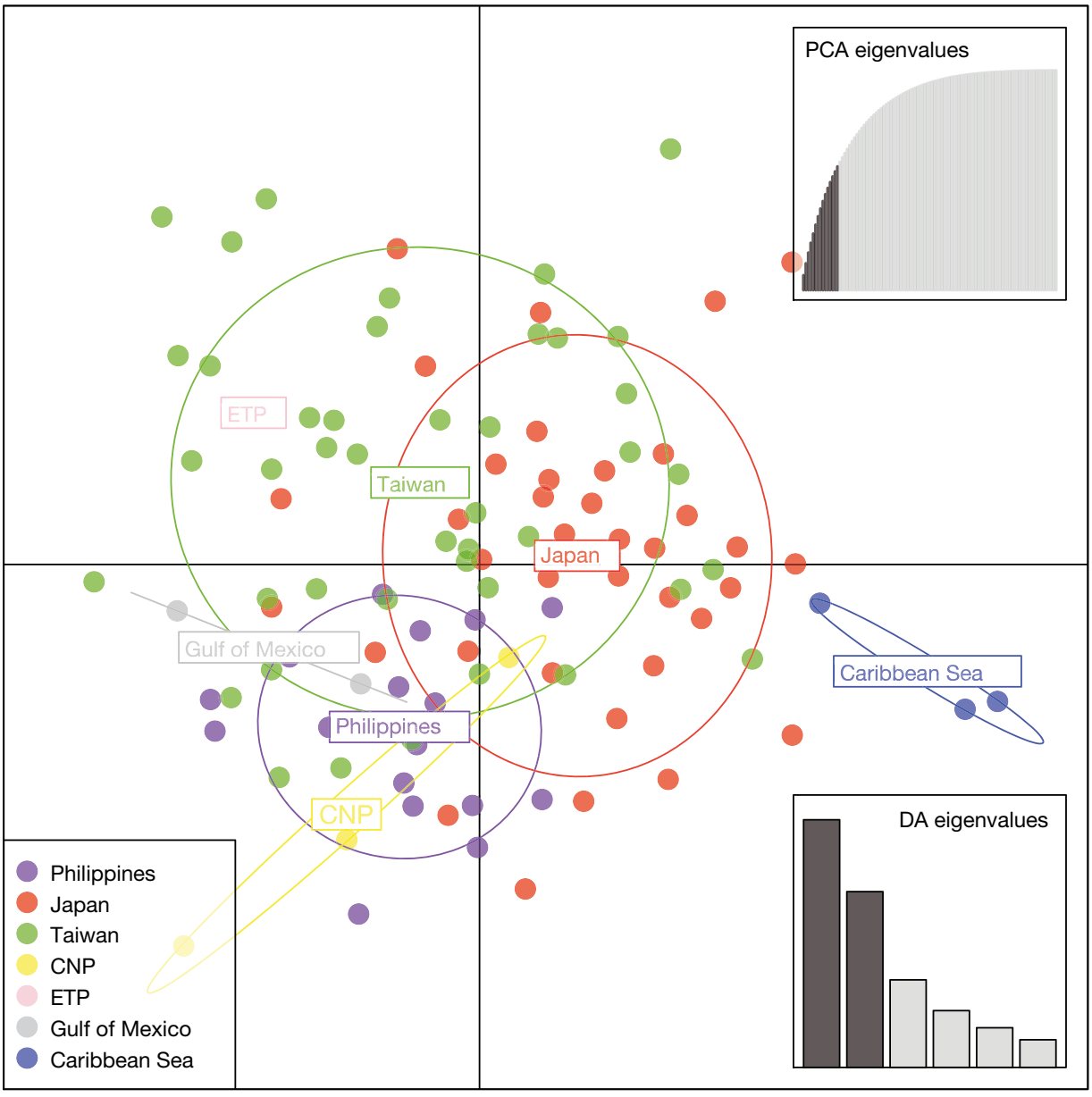

Fig. 2. Discriminant analysis of principal components (DAPC). Individual Fraser's dolphins are represented as dots and groups as ellipses. For the bottom inset of discriminant analysis (DA) eigenvalues, the *x*-axis represents linear discriminants and the *y*-axis represents the corresponding *F*-statistics; for the top inset of principal component analysis (PCA) eigenvalues, the *x*-axis represents the number of retained PCs and the *y*-axis shows corresponding cumulative variance. CNP: Central North Pacific; ETP: Eastern Tropical Pacific (position of single sample indicated by label)

of low-frequency haplotypes, possibly resulting from an historic expansion or selective sweep. When combining all samples from the western North Pacific together, Fu's *F*s was still negative and statistically significant (Table 3).

A non-unimodal mismatch distribution was seen in Japan, Taiwan, and the Philippines (Fig. S5); however, SSD and *r* were small and statistically insignificant (Table 4), suggesting that the distributions concurred with both demographic and spatial expansion models. The estimated time of population expansion was at about the same time for all 3 groups (Table 4), with the time of spatial expansion starting slightly later than the time of demographic expansion. The estimated chronological time for the expansion was 2000–11 000 yr ago (Table 4).

In the pairwise F_{ST} comparisons, significant differentiation was found between the Philippines and

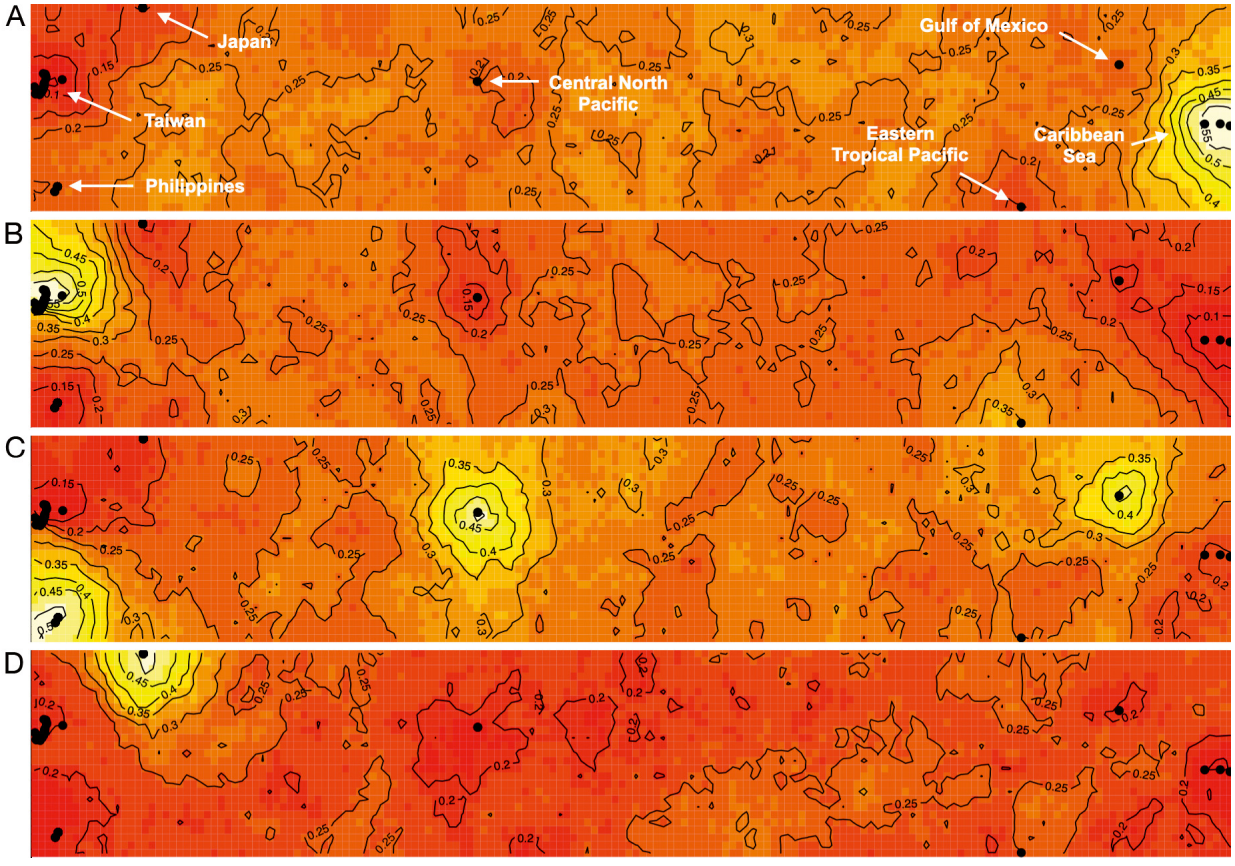

Fig. 3. Result of the Geneland analysis showing the most common pattern of the population membership of Fraser's dolphins when $K = 4$. Panels show the landscape of the range likelihood of each population: (A) Caribbean Sea; (B) Taiwan; (C) the Philippines, central-eastern tropical Pacific, and Gulf of Mexico; and (D) Japan. Note that the population shown in panel C was sporadically distributed in multiple locations. The dots represent the samples, with geographical locality indicated in (A). Probability values shown on contour lines and indicated by colour gradient, where red indicates the lowest probability and white shows the highest probability

Japan (F_{ST} = 0.029, p = 0.026) and between the Philippines and Taiwan (F_{ST} = 0.034, p = 0.022) (Table 5). Comparisons among CNP, ETP, GM, and CS were omitted, as the sample sizes were too small to provide useful inferences. In the Φ_{ST} comparison, on the other hand, none of the paired estimates were statistically different from 0 (Table 5). The exact tests based on both haplotype frequencies and the Tamura and Nei model indicated that the Philippines, Taiwan, and Japan were differentiated (Table S7).

4. DISCUSSION

4.1. Population structure

Population differentiation between Japan and the Philippines was previously recognized from skull morphology: the skulls of Japanese samples were broader and the rostrum wider, with larger orbits and internal nares, and a longer cranium (Perrin et al. 2003). From our genetic data, differentiation was evident between Japan, the Philippines (consistent with the cranial data), and Taiwan from ordination analyses (with some overlap), and for F_{ST} values between Japan and the Philippines or Taiwan. This pattern was supported by the analyses in Geneland (differentiating between Japan, Taiwan, and the Philippines), but the haplotype network showed little indication of lineage sorting among any of the putative populations.

The sample size from the Philippines was comparatively small, but the pattern of differentiation detected by summary statistics (which may be affected by sample size) was generally consistent with ordination methods (which are independent of sample size with respect to the placement of individual points in Euclidean space). In general, F_{ST} values were small

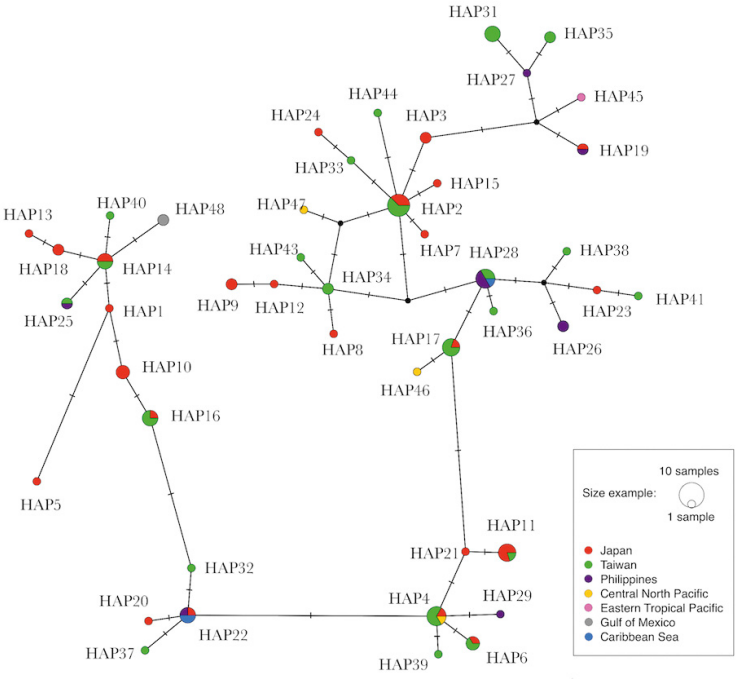

Fig. 4. Median-joining network plot showing the relationship among the mtDNA control region haplotypes of Fraser's dolphins. The circles represent unique haplotypes, with different colours showing the composition of sample origins, and the circle size indicative of the number of individuals with that haplotype (see key). Solid black circles indicate missing intermediate haplotypes, and the hatch marks on the lines indicate the number of mutational steps separating the haplotypes

and of a consistent magnitude, and significantly different from 0 for most comparisons among the western North Pacific putative populations. Ordination methods, which have more power, separated all groups with varying levels of overlap. For mtDNA, both the lack of lineage sorting evident in the network, and the lack of significant Φ_{ST} comparisons (which reflects differences among haplotype sequences) suggest relatively recent division among populations in Japan, Taiwan, and the Philippines.

A number of other marine vertebrate species inhabiting the same or adjacent regions, including common bottlenose dolphins *Tursiops truncatus* (Chen et al. 2017), flathead mullet *Mugil cephalus* (Shen et al. 2011), and green sea turtles *Chelonia mydas* (Jensen et al. 2019), also show similar patterns of structure. For bottlenose dolphins, Chen et al. (2017) proposed that previous glacial events strengthened oceanographic barriers, with differentiation later diminished by the resumption of gene flow when the environment became favourable. In our study, the Philippine samples were collected from the Sulu Sea, a semi-enclosed deep-sea body of water, where most of the Fraser's dolphin sightings have been in waters 700–3500 m deep (Dolar et al. 2006, Dolar 2018). The Sulu Sea was once as shallow as 420 m or less at its edge during the glaciation epochs (Wang 1999, Voris 2000), providing the potential for habitat division during the glacial epochs.

If our samples from Japan reflect a local population, it is possible that the well documented oceanographic differences between Japanese water and the waters around the Philippines or Taiwan (see Miyazawa et al. 2009) could influence dispersion and insularity. However, these samples may be from a transient or migratory population, since Fraser's dolphins are only rarely reported in the temperate waters around Japan (Amano et al. 1996, Kanaji et al. 2017). In contrast, the occurrence of Fraser's dolphins off Taiwan and the Philippines is frequently reported (Yang et al. 1999, Dolar et al. 2006, Tseng et al. 2011). The species most typically has a pan-tropical distribution in deep and offshore waters; however, a more precise distributional range in the broader region is uncertain, due to the scarcity of sightings in the high seas of the western North Pacific Ocean (Kanaji et al.

Table 3. Haplotype counts, genetic (haplotype) diversity (h), nucleotide diversity (π), Tajima's D, and Fu's Fs estimates of a 779 bp mtDNA control region sequence in samples of Fraser's dolphins. Values in parentheses: SD. 'All sequences' include samples from the Central North Pacific, Eastern Tropical Pacific, Gulf of Mexico and Caribbean Sea. Significance is indicated by asterisks ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$)

Geographic group	n	Number variable sites	Number of haplotypes	h	%π	Average number of nucleotide differences (k)	Tajima's D	Fu's Fs
Japan	35	44	24	0.973 (0.014)	0.012 (0.10)	9.689	−0.41	−6.834**
Taiwan	42	40	22	0.958 (0.013)	0.012 (0.07)	9.417	−0.041	−3.197*
Philippines	10	26	7	0.911 (0.077)	0.012 (0.21)	9.044	−0.076	0.64
Western North Pacific	87	61	42	0.973 (0.006)	0.012 (0.06)	9.534	−0.777	−14.233***
All sequences	96	64	46	0.974 (0.005)	0.012 (0.05)	9.588	−0.824	−17.243***

Table 4. Mismatch analysis results for (A) demographic expansion and (B) spatial expansion models for Fraser's dolphins. τ: time since expansion measured in mutational time units; SSD: sum of squared deviation in goodness-of-fit test; *r*: raggedness index; T_1 (T_2): time of demographic/spatial changes for each geographic group calculated using a substitution rate (μ) of 1×10^{-7} (7×10^{-8}). The 95% profile likelihood (confidence interval, CI) for the estimates is given in parentheses

Geographic group	τ (95% CI)	SSD	*r*	T_1 (95% CI)	T_2 (95% CI)
(A) Demographic expansion model					
Japan	13.4 (7.254–17.988)	0.012	0.014	7748 (4195–10 401)	11069 (5992–14 859)
Philippines	12.6 (4.996–17.707)	0.023	0.044	7286 (2889–10 239)	10408 (4127–14 627)
Taiwan	11.5 (5.68–19.568)	0.005	0.011	6650 (3284–11 315)	9500 (4692–16 164)
Western North Pacific	13.1 (6.051–18.041)	0.003	0.004	7575 (3499–10 432)	10821 (4998–14 903)
(B) Spatial expansion model					
Japan	8.396 (4.8–20.161)	0.021	0.014	4855 (2776–11 658)	6936 (3965–16 654)
Philippines	9.042 (5.105–18.239)	0.026	0.044	5228 (2952–10 547)	7469 (4217–15 067)
Taiwan	7.551 (4.547–19.242)	0.01	0.011	4366 (2629–11 127)	6238 (3756–15 895)
Western North Pacific	7.091 (4.265–20.619)	0.009	0.004	4100 (2466–11 923)	5858 (3523–17 033)

Table 5. Pairwise divergence between the 3 main geographic groups of Fraser's dolphins according to mtDNA data. *$p < 0.05$

		F_{ST}		
		Japan	Taiwan	Philippines
Φ_{ST}	Japan		0.01	0.029*
	Taiwan	0.009		0.034*
	Philippines	0.031	−0.017	

2017). Therefore, it is difficult to know the ranging behaviour of the dolphins in our Japanese sample. Further field surveys and genetic sampling covering that region may clarify patterns of connectivity with the group of dolphins found in Japanese waters.

Limited inference for population comparisons could be drawn outside the western North Pacific Ocean, as our sample sizes were small. For instance, even though the results of our DAPC and Geneland analyses appear to support earlier morphological findings suggesting population differentiation between the Pacific and Atlantic Oceans (Perrin et al. 2003), we cannot fully exclude the possibility that this was a stochastic result due to the small number of samples (Halsey et al. 2015). Similar caution is appropriate for inference about putative population differences identified in the central North Pacific, ETP, and GM.

4.2. Population expansion history

Our mtDNA data suggest that Fraser's dolphin populations in the western North Pacific have been expanding, particularly for the population found in Japanese waters. Our estimation for the time of Fraser's dolphin population expansion in the western North Pacific is within the period of most recent deglaciation following the last glacial maximum (19 000–20 000 yr ago; Clark et al. 2009), and most likely at the beginning of the Holocene (about 11 500 yr ago; Mayewski et al. 2004). There is evidence for population expansions during the early Holocene for a number of cetacean species (e.g. Banguera-Hinestroza et al. 2014, Louis et al. 2014, Moura et al. 2014, Chen et al. 2017, 2018). Furthermore, there are clues suggesting range expansion for Fraser's dolphin populations in the modern age. For example, the sighting frequency of this species has increased in recent decades around the Lesser Antilles, the Caribbean (Watkins et al. 1994, Rinaldi & Rinaldi 2011), and the Azores (Gomes-Pereira et al. 2013). The encounter rate of stranded Fraser's dolphins on Japanese coasts has increased somewhat after the turn of the millennium (8 cases during 2000–2018 vs. 3 cases before 2000; National Museum of Nature and Science 2018). Although the trend of climate warming may be associated with these range expansions (see MacLeod 2009), it is uncertain whether the phenome-

non would persist and become widespread around the globe, and what the consequences may be as this tropical species 'invades' higher-latitude waters.

On the other hand, we did not detect an expansion signal for the Philippine population. The relatively high genetic diversity and flat mismatch distribution pattern could imply a long-term stable Philippine population. However, the sampling size for the Philippine population in this study was relatively small (n = 17 for microsatellites and n = 10 for mtDNA), and the inference of population expansion was made solely based on mtDNA sequence variation. Further assessments investigating a broader range of genomic signals with more samples would reveal a more comprehensive picture for the population history of Fraser's dolphins.

4.3. Implications for conservation

Our study shows that at least for dolphins in the western North Pacific, the mtDNA genetic diversity of Fraser's dolphin is high compared to that of other oceanic delphinid species inhabiting the same or adjacent regions (e.g. pantropical spotted dolphin *Stenella attenuata* populations in Taiwan-Southern China waters: h = 0.778–0.888, π = 0.49–0.96%, n = 4–18, Yao et al. 2004; common bottlenose dolphin populations in eastern Asian waters: h = 0.824–0.908, π = 1.368–2.193%, n = 14–160, Chen et al. 2017). We also show that the level of diversity is similar among regions and when putative populations are pooled. High genetic diversity is consistent with large effective population size and the potential for resilience to environmental fluctuations (Frankham 2005). However, we also found relatively fine-scale population genetic structure and evidence for divergence among most regional population samples included in the study. This would imply a need for management strategies that protect regional diversity and the potential for local adaptation. At the same time, further systematic sampling surveys and genotyping for the dolphins in the region (especially from the Philippines), along with better survey data from the Japanese region, would facilitate the generation of more effective conservation management strategies.

Fraser's dolphin is currently considered an offshore, oceanic delphinid species with least conservation concern (Hammond et al. 2012, Jefferson et al. 2015). However, the impact of frequent Fraser's dolphin bycatches (or direct catches) in the Asian and Eastern Tropical Pacific fisheries (Jefferson & Leatherwood 1994, Perrin et al. 2005, Chou 2006, Porter & Lai 2017, Altherr & Hodgins 2018) will warrant reassessment in the context of structured populations in the western North Pacific. Given our preliminary data on differentiation among geographically distant sites, together with the data on relatively fine-scale differentiation in the western North Pacific, further samples from the extensive distribution range of Fraser's dolphins should be a priority. In particular, samples from the ETP, the South Pacific Ocean, the pelagic North Atlantic Ocean, and the Indian Ocean should be included in future studies to assess the species' global population structure and expansion history. If the hierarchical morphological differentiation revealed by Perrin et al. (2003) does reflect population genetic structure, then future studies should find the North Atlantic Ocean population to be the most distinctive, and possibly identify further differentiated populations in the Southern Hemisphere. We also anticipate that, by examining more Fraser's dolphin samples from a broader range, further light can be shed on the effect of global climate change on the dynamics of the world's tropical dolphin populations.

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