Zoological Journal of the Linnean Society, 2021, **191**, 434–453. With 8 figures.

Integrating morphological and genetic data at different spatial scales in a cosmopolitan marine turtle species: challenges for management and conservation

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Received 23 January 2020; revised 18 May 2020; accepted for publication 27 May 2020

Patterns of genetic structure in highly mobile marine vertebrates may be accompanied by phenotypic variation. Most studies in marine turtles focused on population genetic structure have been performed at rookeries. We studied whether

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genetic and morphological variation of the endangered green turtle (*Chelonia mydas*) is consistent geographically, focusing on foraging grounds. An association between population genetic structure and body shape variation at broad (inter-lineage) and fine (foraging grounds) scales was predicted and analysed using mitochondrial DNA and geometric morphometrics. Although genetic and phenotypic differentiation patterns were congruent between lineages, no fine-scale association was found, suggesting adaptive divergence. Connectivity among Pacific foraging grounds found here suggests that temperatures of ocean surface currents may influence the genetic structure of *C. mydas* on a broad scale. Our results suggest that vicariance, dispersal, life-history traits and ecological conditions operating in foraging grounds have shaped the intraspecific morphology and genetic diversity of this species. Considering a range of geographic and temporal scales is useful when management strategies are required for cosmopolitan species. Integrating morphological and genetic tools at different spatial scales, conservation management is proposed based on protection of neutral and adaptive diversity. This approach opens new questions and challenges, especially regarding conservation genetics in cosmopolitan species.

ADDITIONAL KEYWORDS: conservation genetics – evolutionary potential – foraging grounds – geometric morphometrics – morphotypes – natal homing behaviour – natural selection – phenotypic variation.

INTRODUCTION

Climate, behavioural, ecological and oceanographic factors have shaped the geographic distribution and population structure of marine biodiversity in the absence of obvious physical barriers (Palumbi, 1994; Jensen *et al.*, 2019). Although there are examples of genetic homogeneity over long distances in marine systems (Lessios *et al.*, 1998; Lessios & Robertson, 2006; Crandall *et al.*, 2010), other studies have shown population structure in species with high dispersal potential (Viaud-Martinez *et al.*, 2008; Ansmann *et al.*, 2012; Viricel & Rosel, 2014; Van Cise *et al.*, 2019; Jensen *et al.*, 2019).

In highly mobile marine vertebrates without a larval phase (e.g. marine mammals and reptiles), gene flow between populations is determined by behaviour and ecology (Ansmann *et al.*, 2012; Dutton *et al.*, 2014a; Viricel & Rosel, 2014). Factors such as geographic isolation, genetic drift and adaptive divergence may lead to small-scale population structuring (Ansmann *et al.*, 2012; Moura *et al.*, 2014). Patterns of genetic structure may be accompanied by phenotypic variation, including different ecotypes (e.g. prey specialization, social systems and vocal behaviour) and/or morphotypes (e.g. pigmentation, external body structure and shape) (Viaud-Martinez *et al.*, 2008; Moura *et al.*, 2014; Viricel & Rosel, 2014; Van Cise *et al.*, 2019).

Marine turtles are migratory species with a complex life history that includes adult migration from foraging grounds (FGs) to distant breeding areas (rookeries) and ontogenetic changes that affect the distribution of juveniles in a variety of marine habitats (Jensen *et al.*, 2013). The green turtle (*Chelonia mydas* Linnaeus, 1758) has a circumglobal distribution extending throughout tropical and subtropical waters, including hundreds of rookeries and FGs interconnected by a complex network of migratory routes (Avise & Bowen, 1994; Jensen *et al.*, 2013). *Chelonia mydas* exhibits strong natal homing: individuals return to their region of origin for mating and nesting, resulting in rookeries that are genetically differentiated (Allard *et al.*, 1994; Bowen & Karl, 2007). Conversely, FGs frequently aggregate individuals from multiple natal origins (Amorocho *et al.*, 2012; Jensen *et al.*, 2013; Piovano *et al.*, 2019).

Extensive morphological variation has been described for *C. mydas* populations globally, including variation in carapace length, carapace scute patterns, skull morphology and flipper size, among others (Kamezaki & Matsui, 1995; Wyneken *et al.*, 1999; Nishizawa *et al.*, 2010; Seminoff *et al.*, 2015; Coelho *et al.*, 2018). Nevertheless, only two morphotypes, black and light (based on pigmentation and carapace shape), have been widely recognized (Pritchard & Mortimer, 1999; Amorocho *et al.*, 2012; Sampson *et al.*, 2014, 2015; Zárate *et al.*, 2015). Rookeries of these morphotypes seem to be reproductively isolated in the Pacific Ocean (Dutton *et al.*, 2014a; Jensen *et al.*, 2019), but there are FGs such as Galapagos, Costa Rica, Colombia and Japan where both morphotypes exist sympatrically (Hamabata *et al.*, 2009; Amorocho *et al.*, 2012; Heidemeyer *et al.*, 2014; Zárate *et al.*, 2015).

In a previous study based on geometric morphometrics, the carapace shape variation of *C. mydas* was investigated using individuals of three distinct genetic lineages and five FGs from the Pacific and south-western Atlantic Oceans (Álvarez-Varas *et al.*, 2019). This study showed the existence of three morphotypes based on carapace shape, which were concordant with the genetic lineages (Atlantic, western Pacific and eastern Pacific). These results suggested a significant neutral genetic component of carapace shape at a broad geographic scale. Álvarez-Varas *et al.* (2019) also showed well-differentiated morphological groups associated with distinctive FGs. However, genetic differentiation among FGs was not evaluated in this study, thus the influence of neutral genetic processes on carapace shape variation and

other morphological traits at a fine scale (within FGs) remains unknown.

Studying the distribution of genetic diversity and intraspecific morphology is crucial to understanding ecological and evolutionary processes, as well as for biodiversity conservation and management (Avise, 2009; Amaral *et al.*, 2012; Jensen *et al.*, 2019). Whether the genetic and morphological variation of the endangered populations of *C. mydas* is consistent in a geographic context is here studied, and based on this information, conservation and management recommendations are provided. Given previous results indicating a significant neutral genetic component in the carapace shape variation of *C. mydas* (Álvarez-Varas *et al.*, 2019), a positive association between population genetic structure and body shape variation at wide (inter-lineage) and fine (among FGs) scales is predicted. The genetic differentiation patterns between lineages and FGs are expected to agree with morphological trait differentiation, using greater sampling effort and the estimation of population genetic parameters. Specifically, the diversity and genetic structure of *C. mydas* was analysed using mitochondrial DNA (control region) of individuals from ten FGs distributed across the Pacific and south-west Atlantic Oceans, and the morphological differentiation among populations was examined using geometric morphometrics of six external body traits (including carapace, plastron, head and flipper).

MATERIAL AND METHODS

Study area and turtle capture

This study included *C. mydas* FGs located in the south-west Atlantic region (Uruguay); south-central/western Pacific (Fiji and New Zealand, respectively) and eastern Pacific (from north to south: Mexico, Costa Rica, Galapagos, Peru and Chile) (Fig. 1). Details on specific locations and permits are shown in the Supporting Information, Table S1.

Sample collection and genetic analyses

Blood was collected from the dorsal cervical sinus and skin samples were collected using a biopsy punch or a sterile scalpel from the neck or inguinal area (approximately 1 mL of blood and 5 mm diameter of tissue was taken; Álvarez-Varas *et al.*, 2017). All samples (N = 314) were stored in 90% ethanol or saturated salt solutions. DNA was isolated using the salting-out protocol of Aljanabi & Martínez (1997). The control region of mitochondrial DNA (mtDNA) was amplified using primers LCM15382 and H950g designed by Abreu-Grobois *et al.* (2006). The reactions were carried out following Álvarez-Varas *et al.* (2017). Products of PCR were visualized using electrophoresis on 1% agarose gels with GelRed Nucleic Acid Stain (Biotium), purified and sequenced bidirectionally by Macrogen Inc. (Seoul, South Korea). Except for the Fiji samples (which were removed from subsequent analyses due to unsuccessful amplification), analyses were successful in all cases. Analyses were carried out at the Laboratorio de Biodiversidad Molecular, Pontificia Universidad Católica de Chile, Santiago, Chile, and at the Centro de Investigación en Biología Celular y Molecular, Universidad de Costa Rica, San José, Costa Rica (samples from Galapagos and Costa Rica).

Raw sequences were edited manually and polymorphic sites were identified in the sequence chromatograms using SEQUENCHER v.5.4.6 (Gene Codes Corporation, Ann Arbor, MI, USA). Sequences were truncated to a standard length of 765 bp. Sequences were aligned using ClustalX v.2.1 (Thompson *et al.*, 1997), and haplotypes were identified using the BLAST tool implemented in the GenBank database (National Center for Biotechnology Information, USA: NCBI Home page http://www.ncbi.nlm. nih.gov).

Phylogenetic analyses and natal origin classification

Given that FGs host individuals with multiple origins, the haplotype of each individual was first identified and then classified according to its genetic lineage, defined here as 'natal origin'. Thus, genetic lineage or natal origin refers to the origin of each individual according to its control region haplotype (not corresponding to rookery, which is limited to a specific reproductive colony; see below: ATGL, SC/WPGL, NC/EPGL). Regions represent the geographic areas where FGs are located (Atlantic, western Pacific, south-central Pacific and eastern Pacific regions).

Some Pacific FGs host individuals with different genetic lineages (Álvarez-Varas *et al.*, 2019). In order to corroborate extant genetic lineages of *C. mydas* in the Pacific Ocean and then to assign a natal origin to each individual from FGs with greater accuracy, a phylogeny was reconstructed using a total of 241 haplotypes retrieved from GenBank for this ocean basin (recovered from rookeries and FGs; Supporting Information, Table S2). Given that individuals from the Atlantic FG (Uruguay) only had haplotypes corresponding to the 'southern Atlantic lineage' (CMA5.1 and CMA8.1; Shamblin *et al.*, 2012), all turtles in this study from Uruguay were grouped into the 'Atlantic genetic lineage' (ATGL) and haplotypes from the Atlantic Ocean were excluded from the global phylogeny.

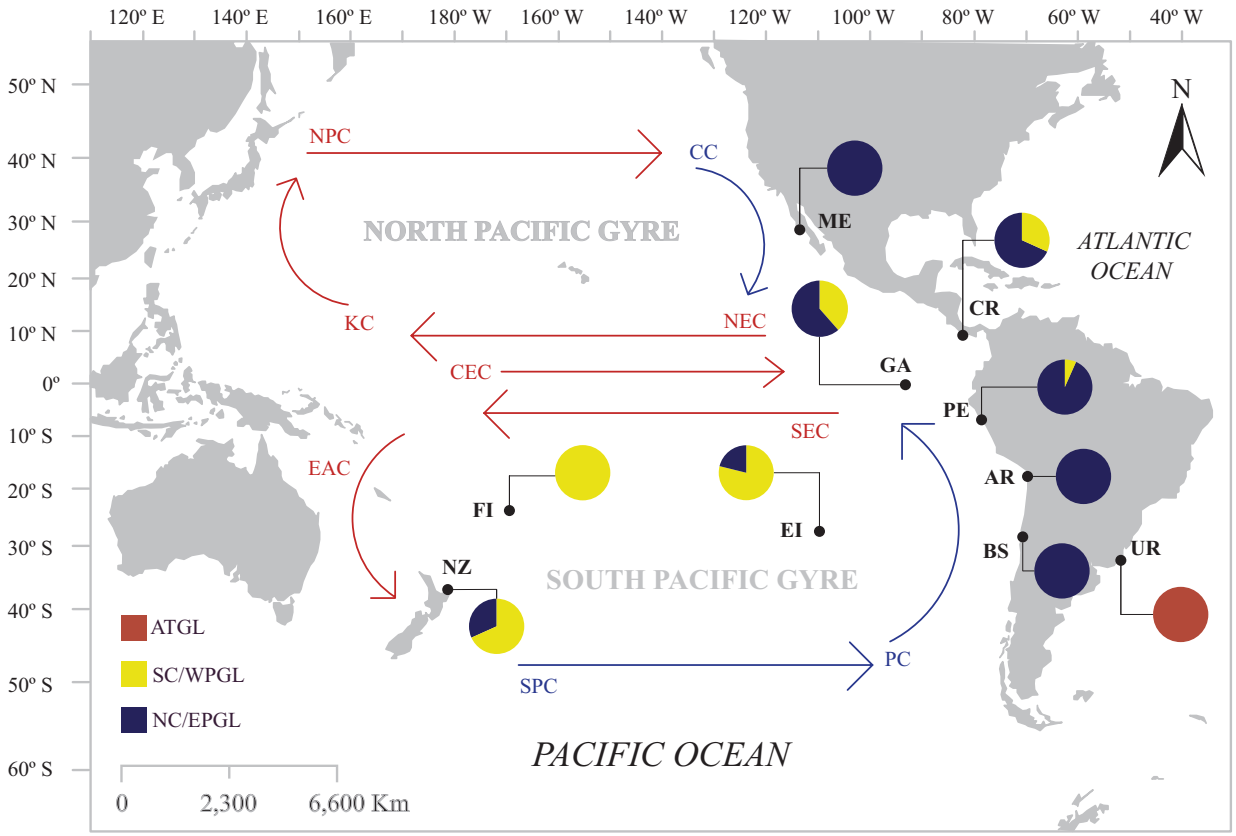

Figure 1. Map depicting the *Chelonia mydas* foraging grounds located in the south-western Atlantic and Pacific Ocean, and the main Pacific surface current systems. Source: own elaboration with data from Tomczak & Godfrey (2013). Red arrows refer to warm currents and blue arrows to cold currents. Pie charts indicate the proportions of each lineage within the foraging grounds. NPC, North Pacific Current; SPC, South Pacific Current; NEC, North Equatorial Current; SEC, South Equatorial Current; CEC, Counter Equatorial Current; CC, California Current; KC, Kuroshio Current; EAC, East Australian Current; PC, Peru Current; ATGL, Atlantic genetic lineage; SC/WPGL, south-central/western Pacific genetic lineage; NC/EPGL, north-central/eastern Pacific genetic lineage; UR, Uruguay; NZ, New Zealand; FI, Fiji; EI, Easter Island (Chile); ME, Mexico; CR, Costa Rica; GA, Galapagos (Ecuador); PE, Peru; AR, Arica (Chile); BS, Bahia Salado (Chile).

Furthermore, to determine the evolutionary relationships between haplotypes found in FGs of this study, phylogenetic trees were inferred using haplotypes identified in our samples from the Pacific and Atlantic Oceans (35 haplotypes in a total of 314 samples). We inferred phylogenetic trees using maximum likelihood and Bayesian inference, with the flatback sea turtle (*Natator depressus*) used as the outgroup (Duchene *et al.*, 2012) (sister-species, GenBank U40662). The software IQTree v.1.7. J (Nguyen *et al.*, 2014) was used to infer maximum likelihood trees, as well as the substitution nucleotide model, and branch support assessed with 1000 bootstraps. According to the Bayesian information criterion (BIC) the best-fit substitution models were TIM+F+I+G4 (transition model with unequal nucleotide frequencies; Rodríguez *et al.*, 1990) and HKY+F+I+G4 (Hasegawa–Kishino–Yano model, unequal transition/transversion rates and unequal nucleotide frequencies; Hasegawa *et al.*, 1985), for the global (241 haplotypes) and specific (35 haplotypes) datasets, respectively. Bayesian phylogenetic trees were inferred with BEAST v.2.6.0 (Bouckaert *et al.*, 2014) using a strict clock model of 0.01751 subs/site/my (Dutton *et al.*, 2014a), and the Yule model of speciation for tree branching. The best-fit model of substitution was HKY+G4 for both the global and specific datasets (most similar available model to the best model selected by IQTree). Two Markov chain Monte Carlo chains were run for 100 million generations and sampled each 10 000 generations for the global dataset, and 50 million generations for the specific dataset. Proper mixing and convergence of the chains were assessed with the program TRACER v.1.7.1 (Rambaut *et al.*, 2014). The maximum clade credibility tree was extracted using TreeAnnotator v.2.6.0.

Genetic diversity and phylogeographic structure

In order to visualize genetic diversity and possible geographic association among haplotypes, a median-joining network (MJN) was constructed in PopArt (Bandelt *et al.*, 1999) using the 35 haplotypes found in the 314 samples analysed in this study. The MJNs were constructed according to natal origin and FG.

Considering information recovered from phylogenetic analyses and MJN, populations were grouped into genetic lineages or natal origins (i.e. wide-scale: Atlantic-ATGL, south-central/western Pacific-SC/WPGL and north-central/eastern Pacific-NC/EPGL) and FGs within each genetic lineage (i.e. fine scale) for all subsequent analyses. Genetic diversity was estimated by calculating the following summary statistics in ARLEQUIN v.3.5 (Excoffier & Lischer, 2010): number of polymorphic sites (S), haplotype number (h), haplotype diversity (Hd) and nucleotide diversity (π) for each genetic lineage and FG within each lineage. Population structure was assessed using pairwise FST for each pair of genetic lineages and FGs in ARLEQUIN v.3.5 software (Excoffier & Lischer, 2010).

Shape analysis

For geometric morphometrics (GM) analyses, populations were also grouped according to genetic lineages (ATGL, SC/WPGL and NC/EPGL) and FGs within each lineage. All FGs were included except Arica-Chile in these analyses (see details in Supporting Information, Table S1).

The shape of six morphological traits was measured: dorsal view of shell ('carapace', N = 540), ventral view of shell ('plastron', N = 399), dorsal view of right flipper ('flipper', N = 247), dorsal view of head ('dorsal head', N = 233), lateral right view of head ('right head', N = 370) and lateral left view of head ('left head', N = 374). All photographs were obtained using a reference scale and landmarks were digitalized with TPS Dig 2.30 software (Rohlf, 2017). The number and location of landmarks of each structure were established according to Casale *et al.* (2017) (Fig. 2). A Procrustes superimposition was applied to the landmark data in order to remove any non-shape variation (Rohlf & Slice, 1990).

Multivariate regressions were carried out for each trait to determine the influence of size on shape (allometry) in each dataset using centroid size (size variable) as an independent variable and shape (Procrustes coordinates) as a dependent variable (Klingenberg, 2016). A permutation test using 10 000 iterations was performed to assess the significance of the influence of size on shape (for an example in carapace allometry, see: Álvarez-Varas *et al.*, 2019).

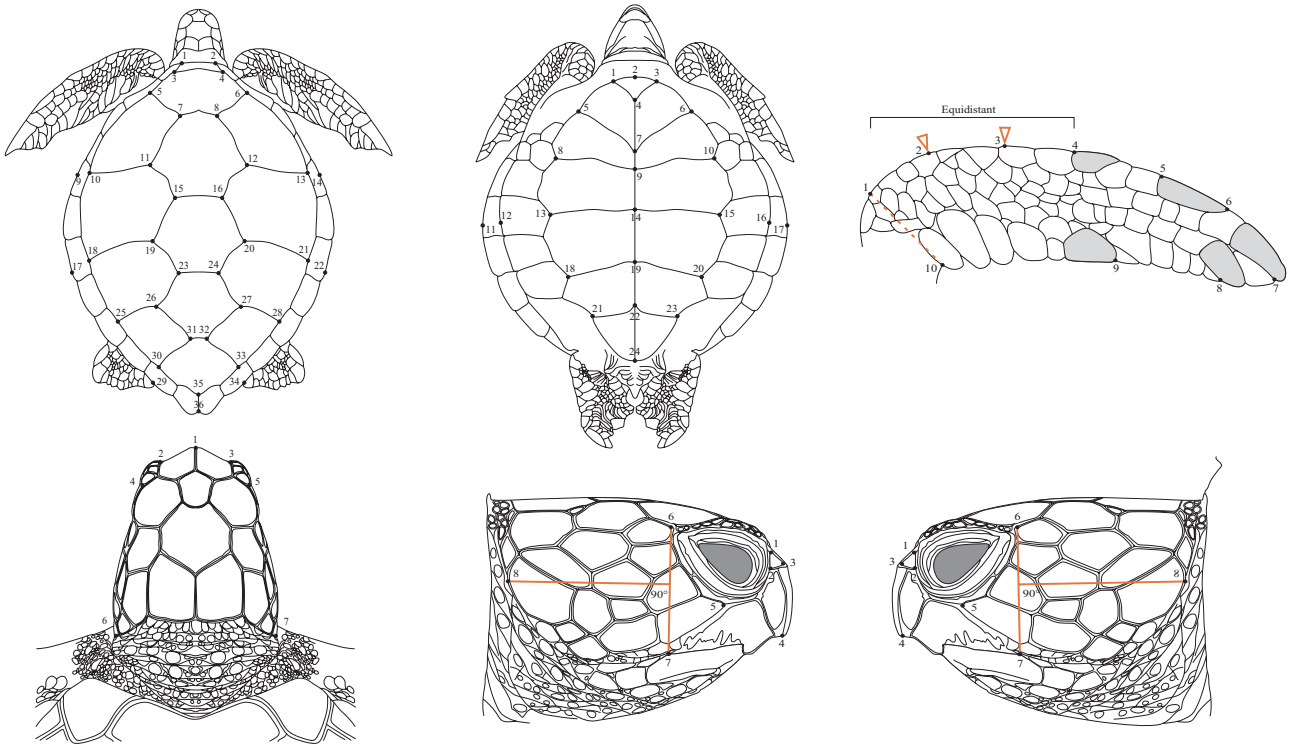

Figure 2. Representation of the landmarks identified on six different body structures of *Chelonia mydas*.

A principal component analysis (PCA) was performed using the covariance matrices of shape variation and the average shape variation between and within genetic lineages (i.e. between FGs). A canonical variate analysis (CVA) was performed to obtain a graphic representation of the data and to discriminate groups based on shape variation in different genetic lineages and FGs. Canonical variate analysis is a multivariate statistical method used to find the shape characters that best distinguish among groups of specimens. The results were reported as Procrustes distances and Mahalanobis distances and the respective *P*-values for these distances after permutation tests (10 000 iterations).

Finally, a Procrustes ANOVA was carried out for each structure to assess the significance of the differences in shape between genetic lineages and between FGs. All analyses were performed using MorphoJ software (Klingenberg, 2011).

RESULTS

Phylogenetic analyses and natal origin classification

Bayesian and maximum likelihood (ML) phylogeny of the global dataset (241 haplotypes) reveal the presence of five well-supported clades associated with the south-central Pacific and western Pacific haplotypes (SC/WPGL), and one major clade grouping the north-central Pacific and eastern Pacific haplotypes (NC/EPGL) (Fig. 3). Maximum likelihood and Bayesian phylogeny of our specific dataset (314 samples) (Fig. 4A) found four clades for the SC/WPGL haplotypes, three subclades within a major clade grouping the NC/EPGL haplotypes and also one clade grouping the Atlantic haplotypes (ATGL; haplotypes not included in the global dataset). The 314 individuals sequenced in this study represent 35 haplotypes; two were classified into the ATGL (N = 14), 11 were classified into the SC/WPGL (N = 89) and 22 into the NC/EPGL (N = 211) according to our phylogenetic analyses (Table 1; Figs 3, 4).

Phylogeographic analyses based on the specific dataset

The MJN according to natal origin using the specific dataset (35 haplotypes) is coincident with the phylogeny, since it exhibits one haplogroup for the ATGL haplotypes, four haplogroups for the SC/WPGL haplotypes and one major haplogroup for the NC/EPGL haplotypes (subclades were not observed) (Fig. 4B). These six haplogroups are well separated by several mutation steps (Fig. 4B). Haplotypes from SC/WPGL are more differentiated than those within NC/EPGL. In addition, the last haplogroup shows a star-like network topology represented by a few highly frequent central haplotypes and various haplotypes of low frequency (Fig. 4B). By contrast, the MJN according to FGs does not exhibit a relationship with the clades (data not shown). Individuals from Pacific FGs have haplotypes corresponding to different lineages, supporting multiple origins (Figs 3, 4). In the Atlantic, turtles exhibit only two haplotypes that belong to the southern Atlantic lineage (see Methods section; Fig. 4).

The number of haplotypes per genetic lineage and FG, and genetic and nucleotide diversity values are shown in Table 1. Haplotype frequencies are included in the Supporting Information, Table S3. Given the small sample size associated with SC/WPGL, all haplotypes were included in a single group. The NC/EPGL shows the highest haplotype diversity, followed by SC/WPGL and ATGL (Table 1). The highest values of haplotype diversity for NC/EPGL are found in Chile and for the SC/WPGL are found in Costa Rica and New Zealand (Table 1). The most common haplotypes for the NC/EPGL are CmP4.1, CmP4.6, CmP4.7; for the SC/WPGL: CmP97.1 and CmP47.1, and for ATGL: CmA8.1 (Supporting Information, Table S3; Fig. 4). Pacific FGs, where both genetic lineages (NC/EPGL and SC/WPGL) are present, exhibit lower haplotype diversity compared to other FGs studied (considering genetic lineages separately; Table 1).

Pairwise genetic difference (FST) results show significant values among all genetic lineages (FST values between 0.7644 and 0.9607; P-value < 0.0001). Moreover, significant differences are observed in New Zealand compared to other FGs within the SC/WPGL; Mexico is different from the other sites within the NC/EPGL (P < 0.05; Fig. 5).

Shape analysis

The results associated with geometric morphometrics analyses according to genetic lineages and FGs are shown in Table 2. Between genetic lineages (i.e. broad scale), morphometrics analyses show high differentiation for all traits except for the flipper (Fig. 6; Table 2). At a fine scale, SC/WPGL exhibits well-differentiated groups for all traits (Fig. 7; Table 2). In contrast, NC/EPGL shows a pattern of differentiation only for the carapace and plastron. The remaining views show high dispersal and overlap between FGs within this lineage (Fig. 8; Table 2).

Mahalanobis and Procrustes distances are significant in all cases when genetic lineages are compared; in almost all cases within SC/WPGL and only in a few cases within NC/EPGL (P < 0.05; Table 2). Procrustes ANOVA show statistical significance for centroid size

Figure 3. Bayesian phylogenetic reconstruction of *Chelonia mydas* control region haplotypes from the Pacific Ocean (765 bp, 241 haplotypes retrieved from Genbank). SC/WPGL, south-central/western Pacific lineage; NC/EPGL, north-central/eastern Pacific lineage; Rookery, haplotype reported in rookeries (i.e. known rookery of origin); Foraging Ground, haplotype reported only in foraging grounds (i.e. unknown rookery of origin, but has not been described as 'orphan' in the literature); Unknown, haplotype retrieved directly from GenBank with unknown locality of reference; Orphan, haplotype that has been described as 'orphan' in published literature (i.e. unknown rookery of origin, based on previous studies); This study, haplotype reported in a foraging ground included in this study.

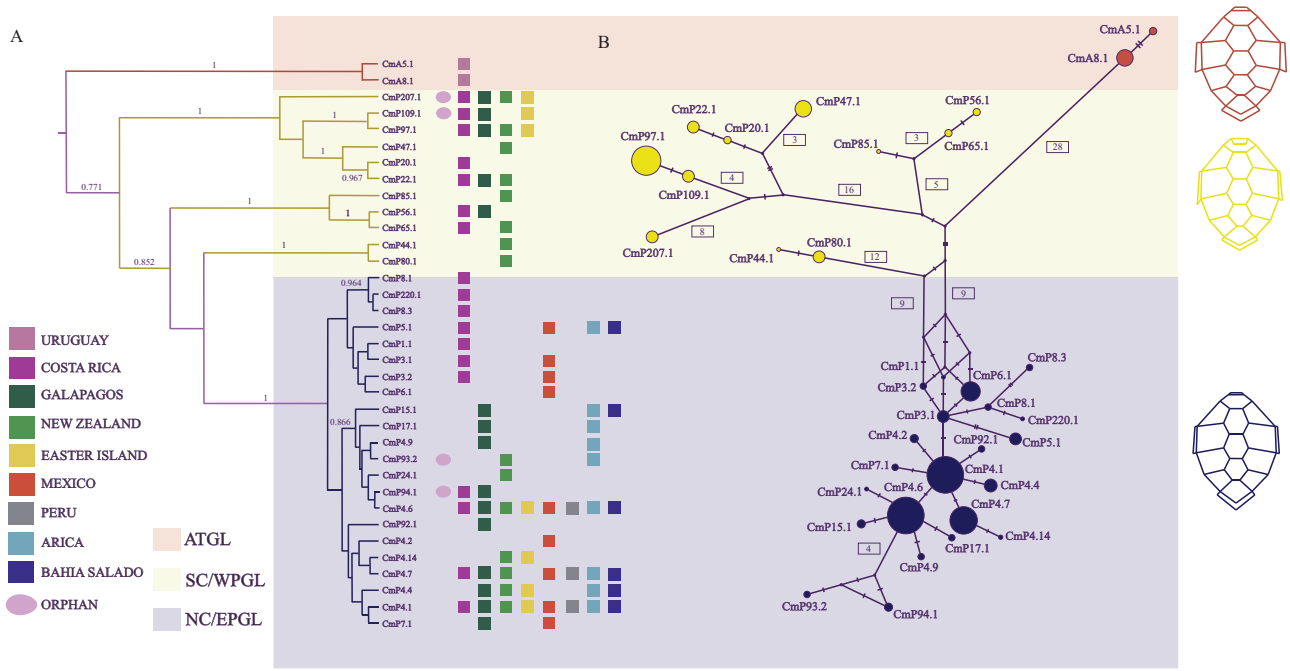

Figure 4. Phylogeographic analyses of *Chelonia mydas* control region haplotypes from Pacific and south-western Atlantic Oceans (this study: 765 bp, 35 haplotypes). A, Bayesian phylogenetic reconstruction. Posterior probability support values are shown at nodes. B, median-joining network (MJN) according to genetic lineages. More than two mutation sites are indicated with a square with the corresponding number of mutated positions. The size of the circles is approximately proportional to haplotype frequency in the dataset. ATGL, Atlantic genetic lineage; SC/WPGL, south-central/western Pacific genetic lineage; NC/EPGL, north-central/eastern Pacific genetic lineage.

and shape for all comparisons except for the plastron comparing FGs within NC/EPGL ($P < 0.05$; Table 2).

DISCUSSION

Our study suggests that gene-flow barriers, ecological, behavioural, climatic and oceanographic factors, have shaped the geographic distribution, population genetic structure and morphological variation of *C. mydas*. Contrary to our predictions, the lack of coincidence between genetic and phenotypic differentiation patterns at a fine scale found, provides insights on a potential adaptive divergence in this cosmopolitan species. Our results integrating genetic and morphological data allow us to propose two management levels for this endangered species globally.

A BROAD-SCALE PICTURE: *CHELONIA MYDAS* LINEAGES AND GENETIC DIVERSITY IN THE PACIFIC AND ATLANTIC OCEANS

Despite the slight differences between phylogenetic trees based on the two datasets (which could be due to the sampling coverage), overall our results were congruent with previous phylogeographic studies in the Pacific Ocean (Dutton *et al.*, 2014a; Jensen *et al.*, 2019). Likewise, MJN agreed with phylogenies, and results for NC/EPGL supported the recent colonization of the eastern Pacific region previously suggested by Dutton *et al.* (2014a) and Jensen *et al.* (2019). Our data was also in accordance with the results of Jensen *et al.* (2019) for the Atlantic Ocean (CmA8.1 being the most common haplotype) and the results of Dutton *et al.* (2014a), who also reported CmP4.1, CmP4.6, CmP4.7 as the most frequent haplotypes for NC/EPGL.

Genetic diversity values found in Uruguay were below those reported for other FGs in this region (Naro-Maciel *et al.*, 2007; Proietti *et al.*, 2012; Prosdocimi *et al.*, 2012), which is probably due to the small sample size used in this study ($N = 14$). In contrast, genetic diversity in the FGs from the Pacific region studied here was higher than in other sites reported for this ocean basin (Table 1), even considering that the individuals were separated according to clades (SC/WPGL and NC/EPGL) within each FG.

The greater diversity in FGs where there is only one lineage (i.e. Arica in Chile and Bahia Salado in Mexico) could imply habitat-use segregation, which has been observed between different size classes (Ballorain *et al.*, 2010) and also has been proposed

Table 1. Mitochondrial control region diversity of *Chelonia mydas* in foraging grounds of this study, compared to other Pacific foraging grounds from published literature. For this study, the region represents the genetic lineages based on the control region haplotypes (Atlantic genetic lineage, south-central/western Pacific genetic lineage and north-central/eastern Pacific genetic lineage) of individuals from foraging grounds. Conversely, for the other studies, the region corresponds to the geographic location of foraging grounds. *N*, sample size; S, polymorphic sites; H, number of haplotypes; h, haplotype diversity; π, nucleotide diversity

Foraging ground	*N*	S	H	h (±SD)	π (±SD)	Reference
South-western Atlantic Region						
Uruguay	14	2	2	0.2637 ± 0.1360	0.0007 ± 0.0006	This study
Subtotal	**14**	**2**	**2**	**0.2637 ± 0.1360**	**0.0007 ± 0.0006**	**This study**
South-central & western Pacific Region						
Costa Rica	20	46	7	0.7789 ± 0.0820	0.0169 ± 0.0089	This study
Galapagos (Ecuador)	25	46	5	0.5733 ± 0.1040	0.0097 ± 0.0052	This study
Peru	1	0	1	-	-	This study
Easter Island (Chile)	15	13	3	0.4476 ± 0.1345	0.0059 ± 0.0035	This study
New Zealand	28	56	9	0.6243 ± 0.1004	0.0185 ± 0.0095	This study
Subtotal	**89**	**56**	**11**	**0.7669 ± 0.0360**	**0.0166 ± 0.0084**	**This study**
Yaeyama (Japan)	142	-	24	0.8360 ± 0.0220	0.0334 ± 0.0167	Nishizawa *et al.* 2013
Ginoza (Japan)	20	-	9	0.8790 ± 0.0430	0.0347 ± 0.0182	Nishizawa *et al.* 2013
Kanto (Japan)	145	-	8	0.7070 ± 0.0460	0.0288 ± 0.0148	Nishizawa *et al.* 2013
Torres Strait (Australia)	99	-	14	0.6050 ± 0.0551	0.0136 ± 0.0069	Jensen *et al.* 2016
Clack Reef (Australia)	45	-	15	0.8687 ± 0.0332	0.0206 ± 0.0104	Jensen *et al.* 2016
Howicks Group (Australia)	76	-	16	0.8256 ± 0.0264	0.0212 ± 0.0106	Jensen *et al.* 2016
Edgecombe Bay (Australia)	85	-	9	0.4807 ± 0.0615	0.0141 ± 0.0072	Jensen *et al.* 2016
Shoalwater Bay (Australia)	90	-	7	0.2624 ± 0.0592	0.0082 ± 0.0044	Jensen *et al.* 2016
Moreton Bay (Australia)	42	-	8	0.3844 ± 0.0954	0.0074 ± 0.0040	Jensen *et al.* 2016
Palmyra Atoll (USA)	349	-	19	0.6190 ± 0.0230	0.0090 ± 0.0050	Naro-Maciel *et al.* 2014
North-central & eastern Pacific Region						
Mexico	52	8	8	0.7255 ± 0.0431	0.0018 ± 0.0013	This study
Costa Rica	32	18	11	0.8024 ± 0.0527	0.0028 ± 0.0018	This study
Galapagos (Ecuador)	54	15	10	0.7813 ± 0.0307	0.0021 ± 0.0014	This study
Peru	14	2	3	0.6593 ± 0.0724	0.0013 ± 0.0011	This study
Arica (Chile)	27	17	9	0.8604 ± 0.0403	0.0030 ± 0.0019	This study
Bahia Salado (Chile)	15	7	6	0.8190 ± 0.0636	0.0019 ± 0.0014	This study
Easter Island (Chile)	4	4	4	1.0000 ± 0.1768	0.0026 ± 0.0022	This study
New Zealand	13	13	7	0.8718 ± 0.0670	0.0035 ± 0.0022	This study
Subtotal	**211**	**28**	**22**	**0.8258 ± 0.0144**	**0.0025 ± 0.0016**	**This study**
Gorgona (Colombia)	55	-	7	0.3000 ± 0.0800	0.0110 ± 0.0060	Amorocho *et al.* 2012
Galapagos (Ecuador)	61	-	11	0.7340 ± 0.0234	0.0010 ± 0.0010	Chaves *et al.* 2017
Machalilla (Ecuador)	43	-	10	0.7490 ± 0.0511	0.0040 ± 0.0027	Chaves *et al.* 2017
Hawaii (USA)	788	-	6	0.4640 ± 0.0180	0.0030 ± 0.0020	Dutton *et al.* 2008
TOTAL	**314**	**86**	**35**	-	-	**This study**

for both morphotypes of *C. mydas* (yellow and black; putative genetic lineages) by some authors (Seminoff *et al.*, 2002; Amorocho & Reina, 2007; Sampson *et al.*, 2014, 2015; Zárate *et al.*, 2015). However, this hypothesis should be tested in future studies.

Our results also showed higher genetic diversity at higher latitudes in the Southern Hemisphere (Chile and New Zealand). However, there is one previous study in the Pacific (Australia; Jensen *et al.*, 2016) where an inverse pattern was observed (i.e. lowest values of genetic diversity in the southernmost FGs). Although these opposing patterns could be associated with the geographic scale in which the analyses were made, future genetic studies involving a greater number of FGs will allow corroboration of the presence of a latitudinal pattern, as well as prioritizing specific conservation areas based on high genetic diversity.

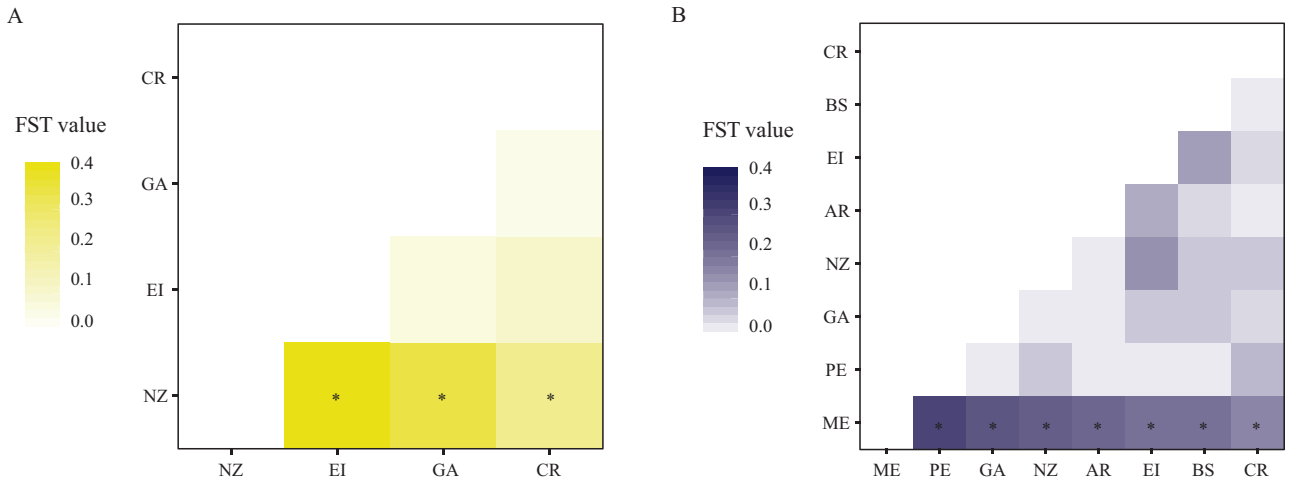

Figure 5. Genetic distance (pairwise FST) among *Chelonia mydas* foraging grounds in the Pacific Ocean calculated using mitochondrial DNA (control region) data and R graphs in Arlequin. A, foraging grounds within the south-central/western Pacific genetic lineage (SC/WPGL). B, foraging grounds within the north-central/eastern Pacific genetic lineage (NC/EPGL). NZ, New Zealand; EI, Easter Island (Chile); GA, Galapagos (Ecuador); CR, Costa Rica; ME, Mexico; PE, Peru; AR, Arica (Chile); BS, Bahia Salado (Chile). *Significant ($P < 0.05$).

Population genetic structure in the Pacific Ocean suggest an influence of surface ocean currents

Foraging ground genetic structuring patterns within each Pacific *C. mydas* lineage may provide insights into the influence of ocean currents on the large-scale dispersal of this species. It has been widely described that ocean surface currents influence sea turtle migrations in all size classes (Luschi *et al.*, 1998; Craig *et al.*, 2004; Bass *et al.*, 2006; Okayuma *et al.*, 2009; Proietti *et al.*, 2012). For instance, Naro Maciel *et al.* (2007) and Proietti *et al.* (2012) suggested that dispersal of *C. mydas* hatchlings and juveniles from Ascension Island to South America are influenced by major equatorial currents of the Atlantic Ocean. Using genetic and Lagrangian drift data, Amorocho *et al.* (2012) observed that equatorial currents may be an important vehicle for dispersal of turtles from western to eastern Pacific regions. Some studies in neonate sea turtles have demonstrated that transoceanic Atlantic migrations coincide with the North Atlantic Subtropical Gyre, a warm-water current system (Putman *et al.*, 2012; Mansfield *et al.*, 2014).

Our results for turtles from the NC/EPGL showed genetic differentiation only in Mexico, which may suggest movement segregation between the Northern and Southern Hemispheres probably modulated by the predominant surface ocean currents, the North Pacific and South Pacific Gyres (Fig. 1). Similar results were obtained by Goetze (2005), who studied two sympatric, circumglobal zooplankton species throughout their global biogeographic ranges and observed that habitat discontinuities at the boundaries of subtropical gyres in the North and South Pacific acted as effective barriers in both species. The genetic homogeneity between New Zealand and the rest of the FGs located in the Southern Hemisphere may provide insights into the influence of colder currents on NC/EPGL turtle dispersal. In particular, the South Pacific Current, an extension of the East Australian Current, may facilitate movements in a west–east direction (Chaigneau & Pizarro, 2005) from New Zealand to South America.

The genetic differentiation found in New Zealand for SC/WPGL turtles suggests these animals do not disperse through the cold South Pacific Current, and thus would present segregation modulated by warm equatorial currents (e.g. North and South Equatorial Currents and Equatorial Counter Current) (Tomczak & Godfrey, 2013; Fig. 1).

As ectotherms, sea turtles are particularly sensitive to environmental temperature. Indeed, studies have reported seasonal movements of *C. mydas* between FGs in order to stay in warmer waters (Avens & Lohmann, 2004; López-Mendilaharsu *et al.*, 2006). The literature corroborates a wider latitudinal distribution for NC/EPGL turtles (Álvarez-Varas *et al.*, 2017; Dutton *et al.*, 2019), suggesting lower thermal constraints than for SC/WPGL turtles. Moreover, NC/EPGL turtles usually have darker carapace coloration (referred to as the black morphotype), which may play an important role in increasing their body temperature (Bustard, 1970).

The hypothesis of movement segregation mediated by temperatures of ocean currents is concordant with the pattern of genetic structure observed in the

Table 2. Results of geometric morphometrics analyses on body shape variation of *Chelonia mydas* according to genetic lineages and foraging grounds within each lineage. ATGL, Atlantic genetic lineage; SC/WPGL, south-central/western Pacific genetic lineage; NC/EPGL, north-central/eastern Pacific genetic lineage; UR, Uruguay; NZ, New Zealand; GA, Galapagos (Ecuador); PE, Peru; CR, Costa Rica; EI, Easter Island (Chile); BS, Bahia Salado (Chile); ME, Mexico; FI, Fiji

Shape variation	Variables	Multivariate regression (%)	*P*-value	PC1	PC2 (cumulative %)	PC3 (cumulative %)	PCA scatterplot description	PCA average shape description	CVA description	Mahalanobis Distances	Procrustes distances	Procrustes ANOVA	
												Centroid size	Shape
According genetic lineages													
Carapace	ATGL-SC/WPGL-NC/EPGL	20.262	< 0.0001	47.210	61.269	73.464	Grouping with high overlap, high dispersal in SC/WPGL and NC/EPGL	Axis 1 differentiate all groups	All groups well defined, moderate overlap between ATGL and NC/EPGL	All significant	All significant	All significant	All significant
Plastron	ATGL-SC/WPGL-NC/EPGL	2.926	< 0.0001	24.445	43.785	57.588	Grouping with high overlap, high dispersal in SC/WPGL and NC/EPGL	Axis 1 differentiate all groups	All groups well defined	All significant	All significant	All significant	All significant
Flipper	ATGL-SC/WPGL-NC/EPGL	5.046	< 0.0001	33.537	54.965	69.054	Grouping with high overlap, high dispersal in all groups	Axis 1 differentiate all groups	All groups well defined, moderate overlap between SC/WPGL and NC/EPGL	All significant	All significant	All significant	All significant
Dorsal head	ATGL-SC/WPGL-NC/EPGL	7.857	< 0.0001	59.097	80.210	85.786	Grouping with moderate overlap between SC/WPGL and NC/EPGL, high dispersal in all groups	Both axis differentiate groups	All groups well defined	All significant	All significant except SC/WPGL-NC/EPGL	All significant	All significant
Right head	ATGL-SC/WPGL-NC/EPGL	5.716	< 0.0001	42.388	66.971	76.610	Grouping with moderate overlap, high dispersal in all groups	Axis 1 differentiate all groups	All groups well defined	All significant	All significant	All significant	All significant
Left head	ATGL-SC/WPGL-NC/EPGL	11.139	< 0.0001	47.557	70.459	79.052	Grouping with moderate overlap between SC/WPGL and NC/EPGL a, high dispersal in all groups	Axis 1 differentiate all groups	All groups well defined	All significant	All significant	All significant	All significant
Within SC/WPGL													
Carapace	CR/FI/GA/EI/NZ/PE	12.409	< 0.0001	45.320	64.608	76.651	Grouping with high overlap, high dispersal in all groups	Both axis differentiate groups	All groups well defined	All significant except EI/GA	Most significant	All significant	All significant

Table 2. Continued

Shape variation	Variables	Multivariate regression (%)	*P*-value	PC1	PC2 (cumulative %)	PC3 (cumulative %)	PCA scatterplot description	PCA average shape description	CVA description	Mahalanobis Distances	Procrustes distances	Procrustes ANOVA	
												Centroid size	Shape
Plastron	CR/FI/GA/EI	3.149	0.0107	27.343	47.639	61.218	Grouping with high overlap, high dispersal in all groups	Axis 1 differentiate all groups	All groups well defined	All significant	All significant	All significant	All significant
Flipper	CR/FI/GA/EI/NZ	3.219	0.0366	40.893	56.667	70.721	Grouping with moderate overlap, high dispersal in all groups	Both axis differentiate groups	All groups well defined	All significant	All significant except CR/NZ	All significant	All significant
Dorsal head	CR/FI/EI/NZ	0.748	0.6754	66.591	83.672	88.206	Grouping with slight overlap, high dispersal in all groups	Axis 1 differentiate all groups	All groups well defined	All significant	Most significant	All significant	All significant
Right head	CR/FI/EI/NZ	1.983	0.1610	39.777	70.208	81.356	Grouping with moderate overlap, high dispersal in all groups	Axis 1 differentiate all groups	All groups well defined, slight overlap	All significant except FI	All non-significant except FI/NZ	All significant	All significant
Left head	CR/FI/EI/NZ	4.516	0.0138	51.778	74.356	81.516	Grouping with moderate overlap, high dispersal in all groups	Axis 1 differentiate all groups	All groups well defined, slight overlap	All significant except CR/EI	All significant except FI	All significant	All significant
Within NC/EPGL													
Carapace	BS/CR/GA/EI/ME/NZ/PE	5.369	< 0.0001	55.792	72.722	81.494	Grouping with high overlap, high dispersal in all groups	Axis 1 differentiate most groups	All groups well defined	All significant except EI/NZ	50% significant	All significant	All significant
Plastron	BS/CR/GA/EI/ME	1.961	0.0080	29.711	52.925	65.256	Unclear grouping due to high overlap	Axis 2 differentiate most groups	All groups well defined	All significant	All significant, except AT/CR	Non-significant	All significant
Flipper	BS/CR/GA/EI/ME/NZ	7.751	< 0.0001	56.351	77.461	84.251	Unclear grouping due to high overlap	Axis 1 differentiate all groups	Groups defined but with high dispersal	Most significant	Most non significant	All significant	All significant
Dorsal head	BS/CR/EI/ME/NZ	1.286	0.4257	56.351	77.461	84.251	Unclear grouping due to high overlap	Axis 2 differentiate most groups	Groups defined but with high dispersal	All significant except CR/ME	All non-significant	All significant	All significant
Right head	BS/CR/EI/ME/NZ	5.716	< 0.0001	48.961	68.819	80.011	Unclear grouping due to high overlap	Axis 1 differentiate all groups	Groups defined but with high overlap	50% significant	Most non-significant	All significant	All significant

Table 2. Continued

Shape variation	Variables	Multivariate regression (%)	*P*-value	PC1	PC2 (cumulative %)	PC3 (cumulative %)	PCA scatterplot description	PCA average shape description	CVA description	Mahalanobis Distances	Procrustes distances	Procrustes ANOVA	
												Centroid size	Shape
Left head	BS/CR/EI/ME/NZ	1.078	0.3521	51.594	69.384	79.456	Unclear grouping due to high overlap	Axis 1 differentiate all groups	Groups defined but with high overlap	50% significant	Most non-significant	All significant	All significant

Pacific Ocean, raising new questions about the effect of certain key environmental variables on *C. mydas* movements between FGs. Although our findings should be tested by extending the sampling design to other size classes, FGs and rookeries, and be complemented with tools such as satellite tracking, mark-recapture, particle modelling and other molecular markers, this information provides evidence on the importance of studying genetic structuring patterns at a broad spatial scale in order to better comprehend the ecology of cosmopolitan species and for effective conservation planning.

Morphological variation and its association with genetic structure at different spatial scales

Our results on morphology show marked broad-scale differentiation between genetic lineages for all evaluated traits (except the flipper), suggesting a substantial neutral genetic effect on these traits (Holderegger *et al.*, 2006; Álvarez-Varas *et al.*, 2019). Thus, it is probable that this morphological differentiation is associated with gene-flow barriers (e.g. Panama Isthmus and oceanographic barrier west of Hawaii) and the natal homing behaviour of this species, which would maintain these populations reproductively isolated. Other studies have also described a strong correlation between morphology and genetics in widely distributed marine species. For instance, Kage (1999) and Van Cise *et al.* (2019) found a marked association between morphology and mtDNA haplotypes in short-finned pilot whales in the Pacific Ocean, and Viaud-Martinez *et al.* (2008) demonstrated morphological, genetic and likely ecological divergence between Black Sea and Mediterranean Sea bottlenose dolphins.

All body traits (carapace, plastron, head and flipper) of SC/WPGL turtles vary between FGs. However, traits are not concordant with the genetic structuring pattern in this lineage (only New Zealand exhibited differentiation). On the contrary, NC/EPGL turtles show congruence between the morphological and genetic patterns (low differentiation between FGs, except for Mexico). These results are probably due to SC/WPGL reflecting an ancient lineage of *C. mydas* (Dutton *et al.*, 2014a; Jensen *et al.*, 2019) that has had considerably more time to differentiate than NC/EPGL. Nevertheless, as there is no marked genetic structuring based on mtDNA in SC/WPGL, it is possible that the morphological variation observed is linked to selective pressures associated with different ecological/environmental conditions operating in each FG. This lack of coincidence may also be attributed to the low statistical power of mtDNA at a fine scale (Teske *et al.*, 2018), which demands future research incorporating molecular markers with greater variability.

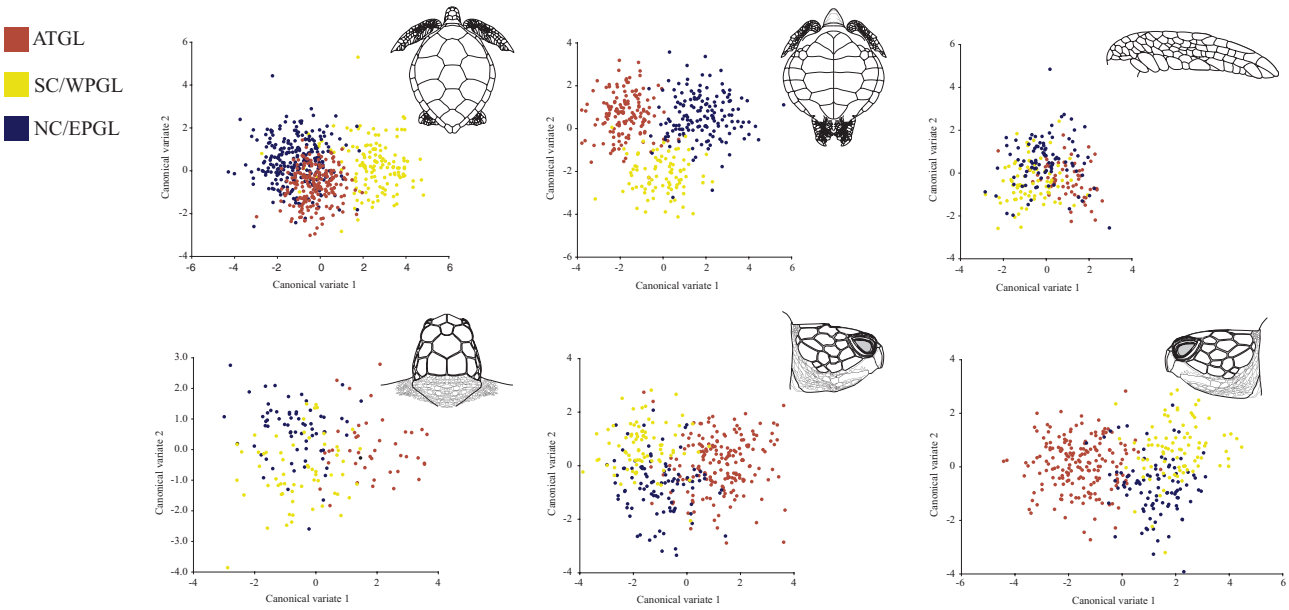

Figure 6. Difference in body shape of *Chelonia mydas* from different genetic lineages. Scatterplot shows the first two axes of the canonical variate analysis for each body structure. ATGL, Atlantic genetic lineage; SC/WPGL, south-central/western Pacific genetic lineage; NC/EPGL, north-central/eastern Pacific genetic lineage. *Carapace analyses have size effect removed.

The hypothesis of natural selection occurring in FGs makes sense, especially for head shape and flipper shape, which are traits that are likely under strong selective pressure since they relate to diet specialization and dispersal capability, respectively (Wyneken *et al.*, 1999; Nishizawa *et al.*, 2010; Coelho *et al.*, 2018). Carapace and plastron shape could be related to ecological or sexual selection (Andersson, 1994; Godley *et al.*, 2002; Bonnet *et al.*, 2010; Salmon & Scholl, 2014; Casale *et al.*, 2017). Genomic tools could allow us to examine the relationship between these phenotypic traits and natural selection, and to rule out the effect of phenotypic plasticity in this endangered species, for which it is difficult to obtain empirical fitness data and carry out experimental studies.

Integrating morphology and genetics: conservation and management implications

It has been demonstrated that FGs have a profound influence on *C. mydas* population dynamics, being key habitats in their life cycle (Solow *et al.*, 2002; Seminoff *et al.*, 2015). Morphological and genetic data confirm that some Pacific FGs aggregate individuals with different origins associated with distinct lineages, which is in accordance with previous reports (Amorocho *et al.*, 2012; Naro Maciel *et al.*, 2014; Godoy *et al.*, 2016; Chaves *et al.*, 2017). In particular, Easter Island (eastern Polynesia), San José (northern Peru) and Matapalito (northern Costa Rica) were documented as new sites harbouring sympatric lineages, and the Reserva de la Biósfera El Vizcaíno (Baja California Sur, Mexico), Arica and Bahia Salado (northern Chile) as FGs hosting individuals from a single lineage.

Understanding the genetic diversity distribution, levels of connectivity between regions and populations, and the processes associated with population structure has important implications for species management and conservation (Avise, 2009; Jensen *et al.*, 2019), especially for *C. mydas*, whose key habitats (FGs and rookeries) are usually separated by hundreds to thousands of kilometres (Seminoff *et al.*, 2015). The high genetic diversity in FGs located at the periphery of the *C. mydas* distribution range (Mexico, Chile and New Zealand) emphasizes the importance of their investigation and protection; particularly in Chile, where anthropic threats are increasing and the population sizes are small or unknown (Álvarez-Varas *et al.*, 2017).

Based on genetic connectivity and morphology patterns found here, focusing conservation and management efforts on two different levels is proposed: (1) genetic lineages and (2) management units (MUs) within genetic lineages.

1. *Genetic lineages:* At a broad scale, the genetic and morphological divergence between NC/EPGL and SC/WPGL *C. mydas* populations corroborates the need for separate management of these lineages in rookeries and FGs (where they are sympatric). Estimation of

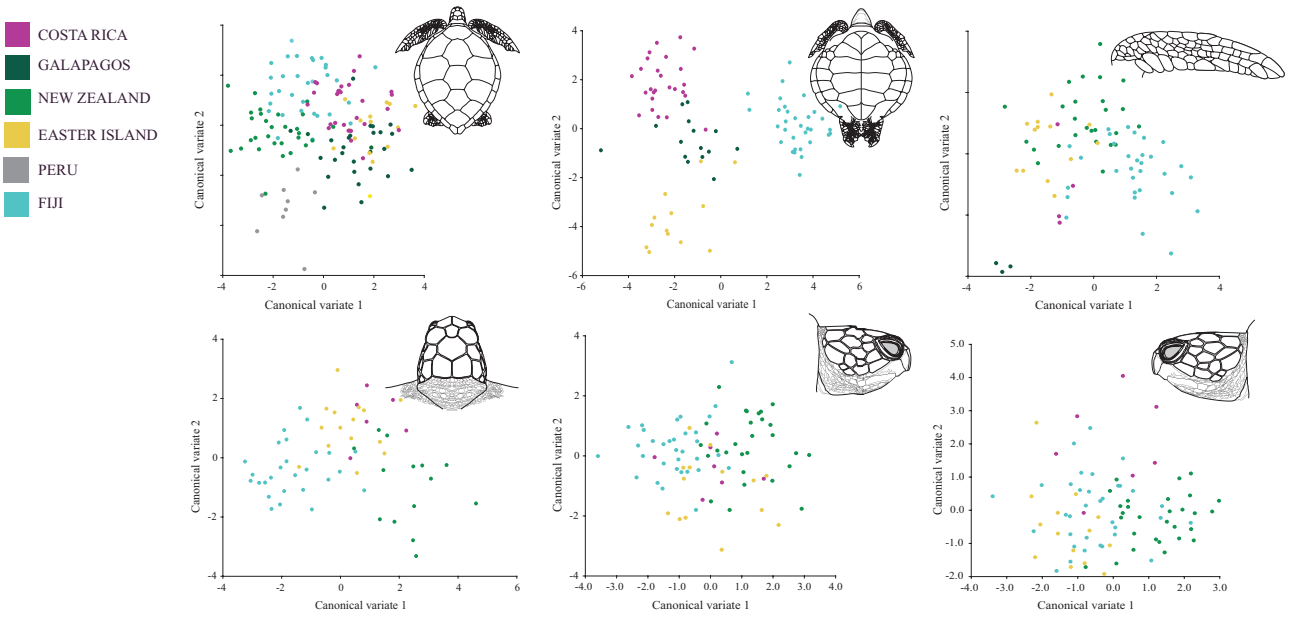

Figure 7. Difference in body shape of *Chelonia mydas* from different foraging grounds within the south-central/western Pacific lineage (SC/WPGL). Scatterplot shows the first two axes of the canonical variate analysis for each body structure. *Carapace analyses have size effect removed.

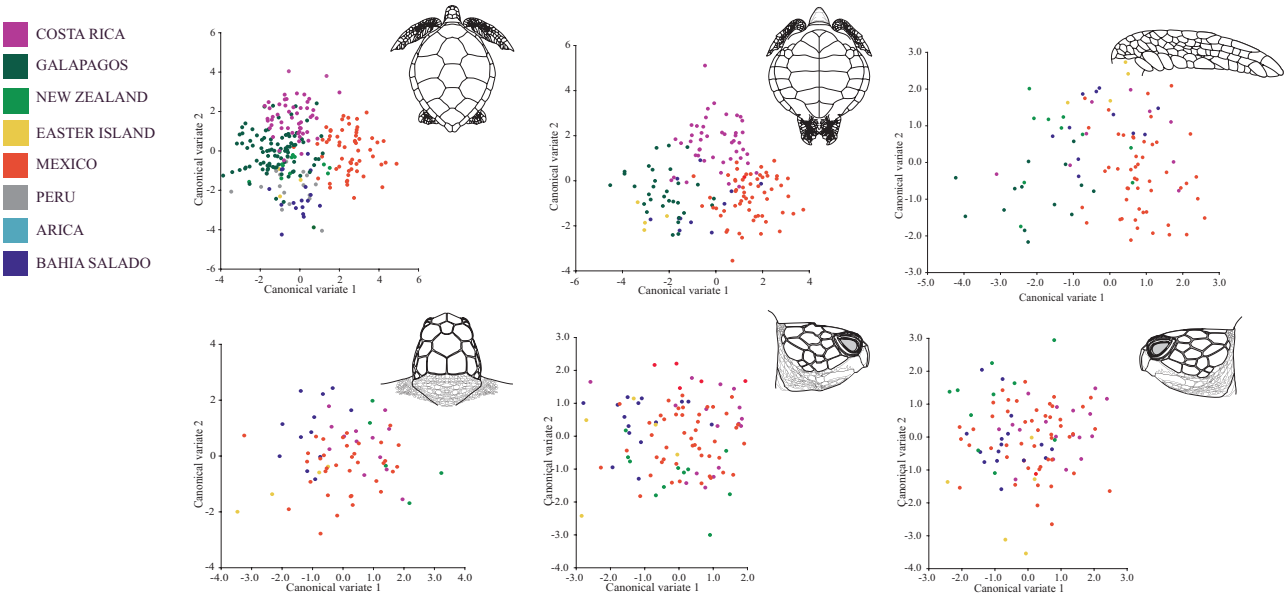

Figure 8. Difference in body shape of *Chelonia mydas* from different foraging grounds within the north-central/eastern Pacific lineage (NC/EPGL). Scatterplot shows the first two axes of the canonical variate analysis for each body structure. *Carapace analyses have size effect removed.

population trends, genetic studies, ecological research and conservation efforts separately, as far as possible, is recommended. Specifically, the evaluation of the NC/EPGL as a separate subpopulation of *C. mydas* in the IUCN Red List. Regarding SC/WPGL and ATGL, further investigation increasing sampling area will provide more evidence to evaluate the segregation of these lineages into subpopulations.

2. *Management Units (MUs) within genetic lineages:* MUs are local populations that are managed

as distinct units since they are genetically and demographically independent (Moritz, 1994). Management unit delimitation in marine turtles has been restricted to nesting rookeries, since they fit the concept of MU (Moritz, 1994; Labastida-Estrada *et al.*, 2019). Nevertheless, the potential effects of natural selection on the morphology of this species suggests including information from FGs in MU delineation in order to maintain locally adapted gene pools and protect important ecological and evolutionary processes. For this reason, it is crucial to integrate data from rookeries and FGs. At this smaller scale, our data only allow us to propose groups of ecologically connected FGs (likely through animal movements). Future research linking these data with previously established MUs (defined using rookery data) will be fundamental to elaborate specific plans. Management unit delimitation using these data will reflect the connectivity between these types of habitats, being key for developing strategies at a regional level, such as the establishment of marine corridors or fishery measures that minimize bycatch rates, among others.

(a) *Foraging grounds within NC/EPGL:* Our results show genetic segregation between hemispheres and a lack of phenotypic differentiation between FGs probably associated with the age of this lineage. Therefore, based on these data, the Mexico FG (Northern Hemisphere) would correspond to a single group, while FGs from the Southern Hemisphere (New Zealand, Costa Rica, Galapagos, Peru and Chile, including Easter Island) would be a separate group of ecologically connected FGs.

(b) *Foraging grounds within SC/WPGL:* SC/WPGL exhibit well-differentiated morphological groups for all traits, but only New Zealand shows genetic differentiation. The genetic data may suggest New Zealand as a single group and Costa Rica, Galapagos, Peru and Easter Island as another. However, considering the lack of coincidence of phenotypic and genetic patterns, extensive genetic and morphological sampling in the south-central Pacific is needed to understand connectivity among FGs and elaborate efficient conservation strategies at a regional level.

Finally, by considering the potential influence of natural selection on the morphological variation in SC/WPGL turtles, research on genes under selection or gene expression, and their relationship to ecological or environmental conditions in FGs, would be useful to understand differences among populations and the selective pressures to which they are subject. All this integrated information will be crucial for long-term protection of the neutral and adaptive diversity and the evolutionary potential of the endangered *C. mydas*.

CONCLUSION

Our study suggests that factors such as vicariance, dispersal, life-history traits and environmental conditions operating in FGs shape the intraspecific morphology and distribution of the genetic diversity of *C. mydas*. Particularly, oceanographic features of main surface current systems in the Pacific Ocean may be influencing the population genetic structure of this species on a broad scale. Although neutral genetic markers are effective at predicting body shape variation in *C. mydas*, the lack of coincidence between genetic and phenotypic differentiation patterns in the FGs suggests adaptive divergence. Such patterns, together with the high genetic diversity and the presence of divergent haplotypes in the FGs, indicate the need to increase ecological research in these areas to solve key questions related to evolution, adaptation and phenotypic plasticity. Finally, based on the Pacific Ocean *C. mydas* genetic structure and morphological variation, management of each lineage separately in areas where they coexist, evaluation of NC/EPGL as a separate subpopulation in the IUCN Red List and integration of the FGs when defining conservation units in order to preserve the evolutionary potential of this species are recommended. By integrating morphological and genetic tools, this study proposes sea turtle conservation management based on the protection of neutral and adaptive diversity, leading to new challenges regarding conservation genetics on threatened cosmopolitan species.

ACKNOWLEDGEMENTS

Financial support for this study was provided by the National Commission for Scientific and Technological Research of Chile (CONICYT), Núcleo Milenio de Ecología y Manejo Sustentable de Islas Oceánicas (ESMOI), National Oceanic and Atmospheric Administration (NOAA), RUFFORD Small Grant, IDEA WILD, Chilean Government Environmental Protection Fund (FPA), the Vice-Rectory of Research of the University of Costa Rica through the Integral Network of Marine Turtles in the Eastern Pacific (RITMA), The Leatherback Trust, Veritas University, Surfari del Mar, Centro de Rescate de Especies Marinas Amenazadas (CREMA), Turner Foundation, National Fish and Wildlife Foundation, DEFRA Darwin Initiative, Sea Life Trust and the Institute

of Natural and Mathematical Sciences, Massey University. Data collection and sampling in Fiji were performed within a project that received funding under award NA17NMF4540081 from NOAA Fisheries PIRO. The statements, findings, conclusions and recommendations are those of the authors and do not necessarily reflect the views of NOAA Fisheries. RA-V gives thanks to CONICYT Beca Doctorado Nacional N° 21160168, Qarapara Tortugas Marinas Chile non-governmental organization's team for their assistance during fieldwork, Riginos Research Group (The University of Queensland) for the useful data/results discussion, and R. Órdenes, C. González, I. Petit, C. Gaymer, M. Ulloa, V. Agurto, S. Espinoza, B. Pincheira and Lafayette Eaton for their support in the field, data collection and the manuscript English revision. Special thanks to A. Pakarati and the Rapa Nui community for allowing us to carry out our research activities on the island. MH thanks members, research assistants and volunteers of the NGO Equipo Tora Carey, F. J. Albertazzi and A. Morales for the constant support of the RITMA project, the Vicerrector of Research of the Universidad de Costa Rica, and R. Blanco and M. M. Chavarria of the Guanacaste Conservation Area for assistance in obtaining research permits. HAB thanks the projects at the Universidad de Tarapacá UTA Proyectos de Pregrado 9720–17 and CONICYT Redes de Investigación REDI170182. ER and ML-U thank H. Fernández-Sanz, J. M. López-Vivas, E. M. Meléndez, O. J. Salazar, N. López, G. A. Aguilar, R. Buelna and L. Ventura, A. Sánchez, F. Castillo, J. Rivera and A. Zaragoza for their support and assistance during fieldwork and logistics. DAG thanks N. FitzSimmons, K. Tarlton and the Department of Conservation and the Northland Community, New Zealand, for their support in the field. JPM-P and DEA-R thank Galapagos Science Center GSC staff, the Directorate of the Galapagos National Park staff, and members and research assistants of the Tortuga Negra Galapagos Project. GMV-R and AF thank Karumbé members, technicians and volunteers that assisted in the fieldwork. SP thanks research assistants and volunteers that collaborated in the project, particularly S. Prakash, M. Tuiono and P. Qarau and Turaga ni Yavusa Ratu Jone Cakau for allowing the research activities to be carried out in Denimanu village's iqoliqoli. PZ gives thanks P. Dutton and his team, Z. Smith, J. Carrion, N. Beaumont, I. Bravo. C. Chasiluisa, M. Robles, C. González, F. Gómez, L. Molina, R. Andrade, S. Castillo, M. A. Fernie, M. Parra, E. Palacios, M. Gonzalez, D. Páez, P. Swannel and other volunteers in the field that worked for the Sea Turtle Project at the Charles Darwin Foundation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Table S1. Details of foraging grounds, capture methods, data collection and research permits used in this study, including references.

Table S2. *Chelonia mydas* control region haplotypes from the Pacific Ocean retrieved from GenBank used in this study (765 bp, 241 haplotypes).

Table S3. Frequencies of *Chelonia mydas* control region haplotypes recovered from foraging grounds included in this study (765 bp, 35 haplotypes). UR, Uruguay; NZ, New Zealand; GA, Galapagos, Ecuador; PE, Peru; CR, Costa Rica; EI, Easter Island, Chile; BS, Bahia Salado, Chile; AR, Arica, Chile; ME, Mexico.