



Evolutionary history of green turtle populations, *Chelonia mydas*, from French Polynesia highlights the putative existence of a glacial refugium

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Abstract

Mapping the distribution of genetic diversity of species over their geographic range is crucial from a conservation perspective. We investigated nesting populations of an iconic and endangered species, *Chelonia mydas*, the green sea turtle, in French Polynesia. Sequences of the mtDNA control region of 97 specimens were analyzed using Bayesian phylogeny reconstruction, Bayesian dating, and skyline plots. Samples from French Polynesia belonged to four of the nine recognized Indo-Pacific lineages, with two lineages (III and IV) recognized as widespread and two other lineages (V and VI) geographically restricted to the South Pacific. More than half of the specimens belonged to the geographically restricted lineages, and suggested the existence of two South Pacific refugia during glacial periods, a western one (represented by lineage V) and an eastern one (represented by lineage VI), herein revealed from French Polynesia. Expansions of populations were recovered in most of the lineages and were all dated after the Last Glacial Maximum, similarly to the Atlantic populations of *C. mydas*. Finally, as the likely existence of a glacial refugium near French Polynesia matches a previously published predicted refugium under future climatic conditions, this makes the area particularly promising for the conservation of green sea turtle populations.

Keywords Phylogeography · Microsatellites · Mitochondrial lineages · South Central Pacific · Population expansion · Last Glacial Maximum

Introduction

Understanding the effects of past climate changes on biodiversity is of the utmost importance in evolutionary

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and conservation biology (Pauls et al. 2013). A historical perspective on the contemporary distribution of genetic diversity is indeed necessary as modern conservation policies must include the conservation of evolutionary processes (Crandall et al. 2000; Moritz 2002) and the areas holding these processes, coined evolutionary hotspots (Vandergast et al. 2008; Hoareau et al. 2013). In this regard, past glacial refugia are particularly important as they usually hold great and/or unique genetic diversity (Hewitt 2004) and shelter therefore a species' adaptive potential. However, in the northern hemisphere, past refugium areas were recently highlighted as the zones most likely to be at risk under future climate conditions (Pauls et al. 2013; Pfenninger et al. 2012; Razgour et al. 2013). It is thus critical to retrace the evolutionary history of species in a spatial context in order to identify endemic lineages and pinpoint past refugium areas. Tracking historical changes in

distribution and abundances enables us to better predict future changes (Fordham et al. 2014).

However, even for iconic and endangered species, such as the green sea turtle, *Chelonia mydas*, our knowledge on genetic distribution and past demographic changes is far from complete. Exemplifying our incomplete knowledge of marine biodiversity, an endemic lineage was only recently recovered from the Ogasawara Islands in the north-western Pacific (Hamabata et al. 2014). This lineage adds up to the eight other mitochondrial lineages reported from the Indo-Pacific region and the two from the Atlantic Ocean (Bowen et al. 1992; Dethmers et al. 2006; Bowen and Karl 2007; Dutton et al. 2014; Jensen et al. 2019). These Indo-Pacific lineages show contrasting distributions, some being widespread (e.g., lineage VIII (formerly clade I) in the Indian Ocean and West Pacific and lineage III (formerly clade V) in the Central and West Pacific) and some more geographically restricted (lineage V (formerly clade II) and lineage VI (formerly clade III) to the South Pacific and lineage VII (formerly clade IV) to the Ryukyu Archipelago and Ogasawara Islands). These contrasting patterns can be explained by the fact that *C. mydas* shows a strong female homing behavior (Bowen et al. 1992) but long-distance migration events have also been reported (Balazs et al. 1995; Luschi et al. 1996; Lohman et al. 1999; Scott et al. 2014).

Regarding past demographic changes, the Atlantic populations of *Chelonia mydas* were recently confirmed to have experienced expansions in the southern and the northern mitochondrial lineages likely following the Last Glacial Maximum (Naro-Maciel et al. 2014). It is particularly important to better understand the effects of past climatic changes as the influence of climate is strong on resources, breeding success, and sex-ratio for marine sea turtles. Indeed, the green sea turtle populations from the Great Barrier Reef have undergone feminization for the past two decades, stronger in the warmer northern sites (Jensen et al. 2018). Additionally, both Hamabata et al. (2014) and Naro-Maciel et al. (2014) point towards the existence of distinct glacial refugia and independent evolution of the lineages, which has important implications for conservation strategy. Reid et al. (2019) recently showed that most lineages of marine turtles underwent population expansions after the Last Glacial Maximum. Similarly, the latest review on phylogeographic patterns of green sea turtles suggests a strong influence of past climatic events, and the survival in multiple glacial refugia during the last glaciations (Jensen et al. 2019).

However, some areas of the species range, such as French Polynesia, have not been thoroughly investigated so far and authors acknowledge the fact that the region is still under-sampled and needs further investigation (Seminoff et al. 2015; Jensen et al. 2019). Dutton et al. (2014) showed that their nine specimens from Mopelia Island, French Polynesia,

belonged to the rare lineage VI. Jensen et al. (2019) also reported on the southern part of the Central Pacific (American Samoa and French Polynesia) as an area of high nucleotide diversity, warranting further investigation. The populations of green sea turtles of French Polynesia, together with that of American Samoa, belong to a distinct population segment (DSP), the Central South Pacific (Seminoff et al. 2015). However, even with limited sampling, there is evidence of spatial structuring between Samoan and French Polynesian green turtle populations (Seminoff et al. 2015). Nevertheless, long-distance migrations between the breeding sites of French Polynesia and the foraging grounds around Fiji and Samoa have been reported on multiple occasions (Balazs et al. 1995; Touren et al. 2018).

Regarding population size, no overall review exists on the number of nesters per island in French Polynesia. Early estimations suggested a total population of 1000 females in French Polynesia (Groombridge & Luxmoore 1989). A recent report on Tetiaroa Island indicates 96 distinct females for the nesting season 2017–2018 and an estimation of 120–130 adult females for Tetiaroa and its islets (Touren et al. 2018). At Scilly Atoll, during the 1970s, 1980s, and 1990s, observations suggested that 300 to 400 females occurred there annually (Lebeau 1985; Balazs et al. 1995). Therefore, the population of French Polynesia is not as large as in other parts of the species range (e.g., Great Barrier Reef), somewhat spatially disconnected, and urgently needs further investigation.

Here, we surveyed the genetic diversity of green sea turtle nesting populations in French Polynesia in order to (i) determine what genetic lineages are present here and thus enabling a better understanding of the global distribution of genetic diversity in this iconic species and (ii) retrace past demographic changes, and verify if their timing matches past climatic fluctuations and the expansion of the Atlantic populations of *Chelonia mydas*.

Materials and methods

Sampling, DNA extraction, and mtDNA control region amplification

Tissue samples were collected from nesting populations of *Chelonia mydas* in French Polynesia (Moorea, Scilly, and Tetiaroa Islands), from both nesting females and hatchlings. Sampling was realized in accordance with relevant guidelines and regulations by Direction de l'Environnement de Polynesie Française, and all experimental protocols were approved by the Haut Commissariat de la République en Polynesie Française (export permit number FR1298700118-E). DNA was extracted from tissue using the QIAextractor robot (Qiagen, Hilden, Germany). A portion of the mitochondrial control region (850 bp) was amplified for 176 specimens

using the primers H950 and LCM15382 and cycling parameters as described in Abreu-Grobois et al. (2006). These specimens are part of a broader study using microsatellite markers to investigate the occurrence of multi-paternity in green sea turtle nests in French Polynesia (unpublished). The mtDNA control region dataset was compared with the microsatellite dataset and paternity results (320 specimens) to keep only one representative of maternal lineage per nest (i.e., removing siblings of the mitochondrial dataset to avoid overrepresentation of some haplotypes), resulting in 97 mtDNA control region sequences used in the subsequent analyses (Online Resources 1). To place the population of French Polynesia in the broader Indo-Pacific context, we analyzed these 97 sequences together with long sequences (i.e., approx. 800 bp) of *Chelonia mydas* from the Indo-Pacific and the Atlantic available in GenBank, mostly from Dutton et al. (2014), Hamabata et al. (2014), and Jensen et al. (2016) (see Fig. 1 for GenBank Accession numbers).

Phylogeny and demography reconstructions

Sequences were aligned using MAFFT online (Katoh et al. 2002). MRAC (Nylander 2004) was used to determine the best-fit model of nucleotide substitutions. Neighbor joining and maximum likelihood reconstructions were performed using Mega v.5.05 (Tamura et al. 2011), with a bootstrapping procedure. The software BEAST v1.8 (Drummond et al. 2012) was used to perform Bayesian phylogenetic reconstructions. Bayes factors were used to choose between 3 clock models (strict, lognormal relaxed, exponential relaxed) and two tree models (coalescent constant size and exponential growth). Following Formia et al. (2006) and Naro-Maciel et al. (2014), a mean mutation rate of 1.75×10^{-8} substitutions/site/year was used to estimate the “Time to the most recent common ancestor” (TMRCA) of each lineage and of the species. A total of 10^7 generations was run, recorded every 100th generation. TRACER v1.5 (Rambaut et al. 2014) was used to ensure sufficient samples were recorded (i.e., ESS > 200) and to obtain parameter estimates. TREEANNOTATOR was used to summarize the information from 10,000 trees. Furthermore, the Bayesian Skyline Plot framework available in BEAST was used to reconstruct past demographic changes of the different lineages separately. Similar to the previous step, 10^7 generations were performed, recorded every 100th generation, using the same mutation rate. TRACER v1.5 was used to compute the Bayesian Skyline Plots. The X-axis indicates the time in years while the Y-axis indicates the relative female effective population size (NeT, with T = generation time).

Nuclear data

Additionally, the 97 specimens were also analyzed at 12 microsatellite markers. Microsatellite markers, as well as

amplification and cycling parameters, were from Dutton and Frey (2009) and Fitzsimmons et al. (1995). Principal coordinates analyses and estimation of population differentiation indices were performed in GenAlex v6.502 (Peakall and Smouse, 2012) to verify if grouping of samples occurred according to the mitochondrial lineages they belong to or according to their geographic origin.

Results

Lineages present in French Polynesia

The sequences of 97 *Chelonia mydas* individuals collected from French Polynesia corresponded to nine haplotypes (Online Resources 1). They belong to four of the nine lineages known from the Indo-Pacific region (Fig. 1). Noticeably, 50 of the 97 sequences belong to lineage VI, while one sequence belongs to lineage V, 44 sequences belong to lineage III, and two sequences belong to lineage IV. So far, lineage VI was only recovered from seven individuals from the Great Barrier Reef, 20 from New Caledonia, nine from Mopelia (French Polynesia), four from American Samoa, one from the Marshalls, and one from Palau at breeding sites (Fig. 2), while another 38 specimens from foraging grounds of eastern Australia also belong to this lineage. While the sequences belonging to lineage IV, V, and lineage VI correspond to known haplotypes (CmP186.1, CmP65.1, and CmP56.1, see Online Resources 1), two of the six haplotypes of lineage III represent new haplotypes (see Online Resources 1; GenBank accession numbers: MH893824–MH893825).

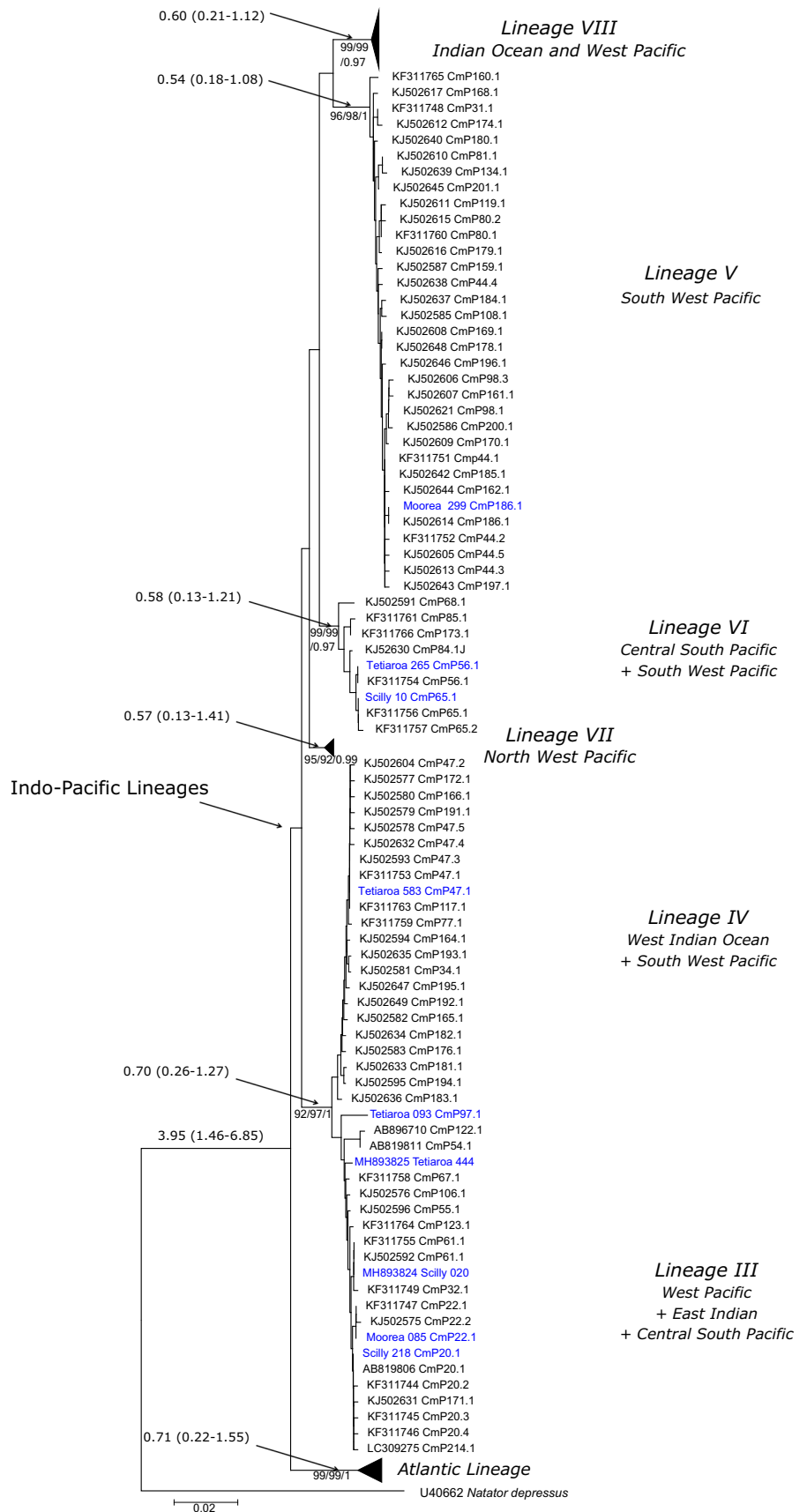
Bayesian dating and Bayesian skyline reconstructions

The TMRCA of all lineages belonging to *C. mydas* was estimated at about 4 My (Fig. 1). TMRCA of each lineage ranged between 0.54 and 0.71 My. The Bayesian Skyline Plot analyses revealed an expansion of populations for all Indo-Pacific lineages except lineage VI (Fig. 3). The expansion events were all estimated to have occurred after the LGM (about 10,000–15,000 years ago).

Nuclear data

The 97 specimens from lineages III, IV, V, and VI analyzed at the 12 microsatellite loci form a homogeneous group on the PCoA with no clustering of specimens according to their lineage (see Online Resources 2: Fig. S1a). Similarly, when considering the three islands analyzed, Moorea, Scilly, and Tetiaroa, specimens cluster together on the PCoA and do not show genetic segregation (see Online Resources 2: Fig. S1b). The F_{ST} values were all low and all but one non-significant,

Fig. 1 Maximum likelihood phylogenetic reconstruction of *Chelonia mydas* mtDNA control region haplotypes. Numbers above branches are “Time to the most recent common ancestor” (TMRCA) in million years and their 95% highest posterior probabilities from the Bayesian reconstruction. Numbers below branches are bootstrap values for the neighbor joining reconstruction/bootstrap values for the maximum likelihood reconstruction/posterior probabilities of the Bayesian reconstruction. The nine haplotypes recovered from French Polynesia specimens are indicated in blue



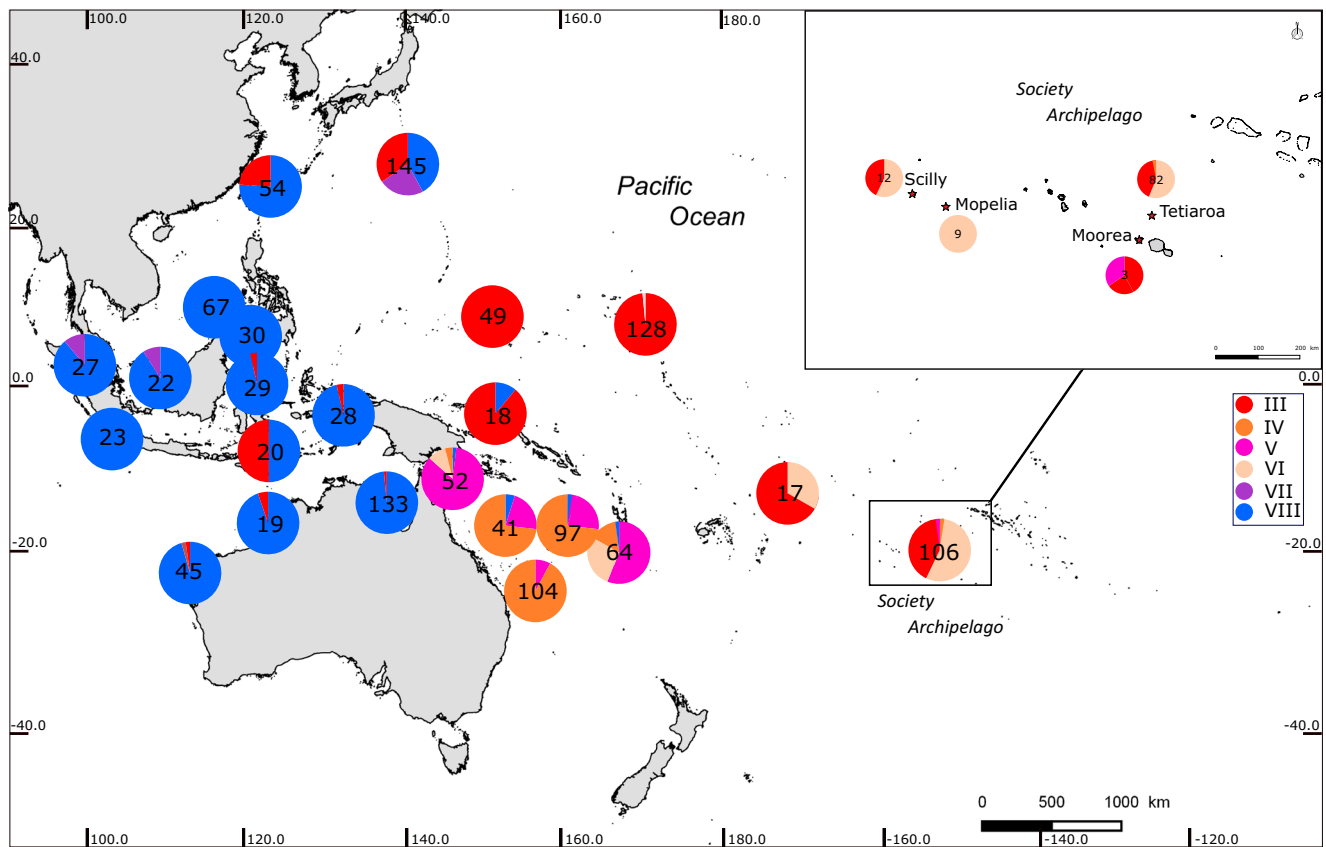


Fig. 2 Frequencies of observed lineages of *Chelonia mydas* in French Polynesia from this study (Scilly, Moorea, and Tetiaroa). Frequencies of lineages in breeding sites of other regions are compiled from Dethmers et al. (2006), Dutton et al. (2014), Hamabata et al. (2014), and Jensen et al. (2016). Numbers in pie charts indicate the number of specimens

sequenced. Numbers along the map frame indicate longitude and latitude coordinates. Map generated with QGIS Lyon (version 2.12.3) a Free and Open Source Geographic Information System, available at <http://www.qgis.org/fr/>

suggesting important gene flow between islands and lineages (see Online Resources 2).

Discussion

Current geographic distribution of mitochondrial lineages

Combining our data with other data available for *Chelonia mydas* from the Indo-Pacific region (Figs. 1 and 2) confirmed three common and widespread lineages (III, IV, and VIII), and three rare and geographically restricted lineages (V, VI, VII). Lineage VIII, common, and occurring from the eastern coast of Africa to the western Pacific, was confirmed absent from French Polynesia. Lineage VII, so far endemic to the north-western Pacific (Hamabata et al. 2014), was also absent from French Polynesia. Lineage III, widespread from the eastern coast of Africa to the south-central Pacific, was present in our dataset. Roughly half of our sequences belonged to this widespread lineage, with two new haplotypes. Two specimens

belonged to lineage IV, a lineage present in the Southwest Pacific and the Southwest Indian Ocean, thus now expanding the range of this lineage to southern part of the Central Pacific. Specimens from lineage V were mainly derived from Australasian populations (Dethmers et al. 2006; Dutton et al. 2014). This lineage range is now extended to French Polynesia as one of the adult specimens analyzed here belongs to this lineage and suggests long-distance migration between the two regions. Long-distance migrations between west and central Pacific islands were already reported from tagged *C. mydas* individuals (Balazs et al. 1995; Touron et al. 2018). Lineage VI is rare and mostly restricted to the South Pacific, with most of the specimens sampled in French Polynesia and New Caledonia. Interestingly, more than half of our sequences belong to this rare lineage and French Polynesia could thus represent the center of the range for this lineage. Similarly to green sea turtles, the hawksbill turtle, *Eretmochelys imbricata*, shows five Indo-Pacific lineages with contrasting distribution patterns that demonstrate the complex evolutionary history of these species linked to paleoclimate changes in the region

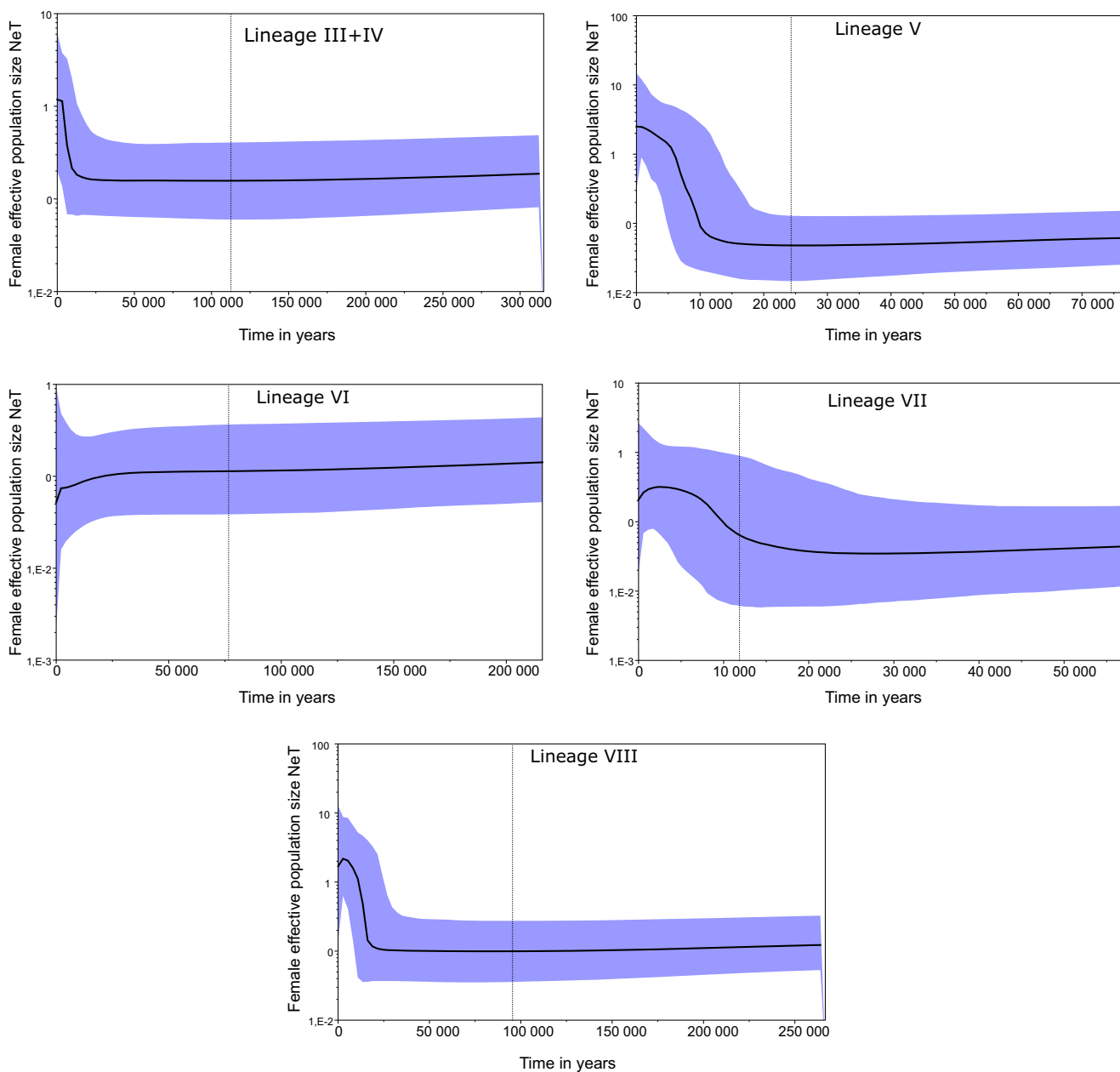


Fig. 3 Bayesian skyline plots reconstructed from all *Chelonia mydas* mtDNA control region sequences belonging to the Indo-Pacific lineages LVIII to LVIII. The X-axis indicates the time in years; the Y-axis indicates the female effective population size (NeT, with T = generation time). The

vertical dotted lines indicate the lower 95% highest posterior density of the root height (i.e., time to the most recent common ancestor of each lineage)

(Vargas et al. 2016). More recently, both Reid et al. (2019) and Jensen et al. (2019) emphasized the complex evolutionary history of sea turtles linked to paleoclimates and their survival in multiple refugia.

Past demographic changes

Signs of population expansions were detected in all lineages except lineage VI. These demographic events were all estimated between 10,000 and 15,000 years ago, after the Last

Glacial Maximum (LGM, Fig. 3). This is in accordance with populations of *C. mydas* from the Atlantic where the expansions of the southern and northern lineages were also both dated after the LGM at about 20,000 years ago (Naro-Maciel et al. 2014). Similarly, many marine organisms showed an expansion of their populations after the LGM, when conditions became more suitable and habitats were newly available (Provan and Bennett 2008; Boissin et al. 2016). In particular, hawksbill and leatherback turtles also showed expansion of their populations dated after the LGM (Molfetti et al. 2013;

Vargas et al. 2016). This is also in accordance with a recent review on population co-expansions of most sea turtle lineages, dated after the LGM (Reid et al. 2019). In contrast, lineage VI did not show a signature of expansion. It is not clear if this lack of signature comes from this lineage having a constant population size over time or if it is from the fewer number of specimens recorded from this rare lineage so far (Dethmers et al. 2006; Jensen et al. 2016). Small sample sizes are known to affect demographic reconstructions (Grant 2015). However, the shape of the network for this lineage is not star-like as the other lineages and this lineage might have a more complex evolutionary history (Jensen et al. 2019: Fig. 3). Overall, these signals of expansion of populations and the occurrence of distinct mitochondrial lineages highlight the sensitivity of green turtles to climate fluctuations (Reid et al. 2019; Jensen et al. 2019).

Past refugium areas, adaptive potential, and conservation units

Endemic or geographically restricted lineages are particularly interesting as they should point towards the areas of former refuges (Avice 2000). A northern refuge was recently suggested for the endemic lineage VII of Ogasawara Islands, Japan (Hamabata et al. 2014). In our study, French Polynesia was shown to shelter four lineages of green sea turtles. The presence of the geographically restricted lineages V and VI, mainly found in the South Pacific Ocean, points towards the putative existence of refugium areas. Found primarily in the South West Pacific, lineage V might have evolved from a western South Pacific glacial refugium, near New Caledonia and northeastern Australia where a glacial refugium area was already suggested for several species (Wörheide et al. 2002; Lukoschek et al. 2007; Tillett et al. 2012). Furthermore, with many specimens of our study belonging to lineage VI, a glacial refugium seems also likely in the south-central Pacific, possibly near French Polynesia. Even if this lineage is present in eastern Australia, it is minor over the thousand green sea turtles sampled (Dethmers et al. 2006; Jensen et al. 2016). However, private haplotypes belonging to this lineage and restricted so far to the south west Pacific exist (see Jensen et al. 2019). The structure of this lineage seems to be complex, and this lineage could have survived in several localities of the south and central west Pacific. Specimens of this lineage present in Australia and New Caledonia could represent a relict population. Alternatively, specimens from the Southwest Pacific could have colonized French Polynesia, where only two haplotypes have been recorded so far. Studies of an increasing number of specimens from this lineage might help understand better its complex evolutionary history. Nevertheless, Polynesia was already suggested as a likely glacial refuge during the LGM for a goby fish (Hoareau et al. 2012). Additionally, Jensen et al. (2019) recorded a high nucleotide diversity in the south-

central Pacific (American Samoa and French Polynesia) and pinpointed the region as a likely past refugium area for green sea turtles. Overall, these results suggest that the two green sea turtle populations from French Polynesia and eastern Australia each have a unique evolutionary history, resulting from distinct glacial refugia. These evolutionary significant units match the regional management units defined for green sea turtles in the South Pacific region (Wallace et al. 2010, Seminoff et al. 2015; Jensen et al. 2019), and thus, the long-term and short-term conservation needs (Moritz 1994) coincide in this region for *C. mydas*. This distinctiveness due to an independent genetic history could provide promising adaptive potential under future climatic conditions, particularly given that the mitochondrial genome codes for important enzymes of metabolic pathways (such as cytochrome oxidases and ATPases). Duchene et al. (2012), studying complete mitogenomes, revealed differences between the Atlantic and Indo-Pacific lineages of *C. mydas*, whose effects on adaptive potential remain unknown so far. Finally, it is particularly interesting to note that French Polynesia is projected to serve as a refuge under future climatic conditions (van Hooidek et al. 2013; Freeman 2015). Regarding sea turtles, a refuge under future warm conditions would likely lower the impact on habitat availability (availability of beaches to lay eggs) and will possibly limit feminization of populations linked to warming. Areas that align with past glacial refugia and those predicted to serve as refugia under future climatic conditions should be a priority for conservation, as they have the potential to maximize the preservation of genetic diversity and unique genetic lineages.

Conclusions

Four of the nine Indo-Pacific lineages were recovered from these French Polynesian specimens. This study extends the range of lineage V and confirms the absence of lineage VIII in the South-Central Pacific. As half of our sequences belong mainly to a rare lineage (VI), this could suggest that French Polynesia was a former glacial refugium for green sea turtles. Past climatic change effects can be seen on most of the lineages that show signs of population expansion dated after the Last Glacial Maximum, similar to the Atlantic populations of *C. mydas*. This study confirms the unique evolutionary trajectory of French Polynesian and eastern Australian populations of green sea turtles. Finally, French Polynesia seems a key conservation area for *C. mydas*; given that it was likely a past glacial refugium, it is predicted to be a refugium under future warm conditions and that four of the nine Indo-Pacific lineages of *C. mydas* occur there.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgments, if applicable.

Data availability The datasets generated during and/or analyzed during the current study are available in the GenBank repository (MH893824–MH893825) and NOAA SWFSC Cmp (haplotype number Cmp21.1 and Cmp249.1).

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