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Evolutionary ecology of sea turtles

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Chapter 6

Synthesis

Jurjan P. van der Zee

Chapter 6

In the present thesis, I investigated the genetic diversity and structure of green and hawksbill turtles to unveil the intrinsic and extrinsic processes that shaped the ecology and evolution of sea turtles. I focused on the in the Atlantic and Southwest Indian Ocean. The thesis can be divided into two sections: an ecological section (Chapters 2 and 3) that deals with the contemporary movements of juvenile sea turtles across the seascape and an evolutionary section (Chapters 4 and 5) that focuses on the phylogeography and demography history of sea turtles in relation to past environmental and climate changes.

In Chapter 2, mitochondrial DNA sequences were used to study temporal variation in juvenile recruitment to a feeding ground located in the southern Caribbean. Chapter 3 dealt with the question how ocean currents influence juvenile sea turtle dispersal, which was assessed in the Southwest Indian Ocean by screening variation in mitochondrial DNA diversity at a feeding ground located in the southern Mozambique Channel. In Chapter 4, the impact of past glacial cycles on the phylogeography of Atlantic and Southwest Indian Ocean green turtles was investigated using genome-wide nuclear data. Chapter 5 concerned the investigation of past changes in genetic diversity, using genome-wide SNPs, in relation to past changes in shallow marine habitat area, as a result of sea level fluctuations, during the Pleistocene in Caribbean hawksbill turtles.

In this concluding chapter, I discuss the main findings and conclusions of each chapter and provide a final concluding remark.

Genetic monitoring at feeding grounds reveals increased juvenile recruitment from recovering populations and provides important insights in meta-population dynamics

In Chapter 2, I presented a study on temporal changes in the genetic composition of a population of juvenile green turtles at a major feeding ground in the southern Caribbean (Lac Bay, Bonaire, the Caribbean Netherlands) in relation to population trends at Caribbean rookeries. Temporal changes in mitochondrial DNA haplotype frequencies were detected at the Lac Bay feeding ground between 2006 and 2016. Most notably, mitochondrial DNA haplotypes associated with rookeries in the northwestern Caribbean increased in frequency toward the end of the study period.

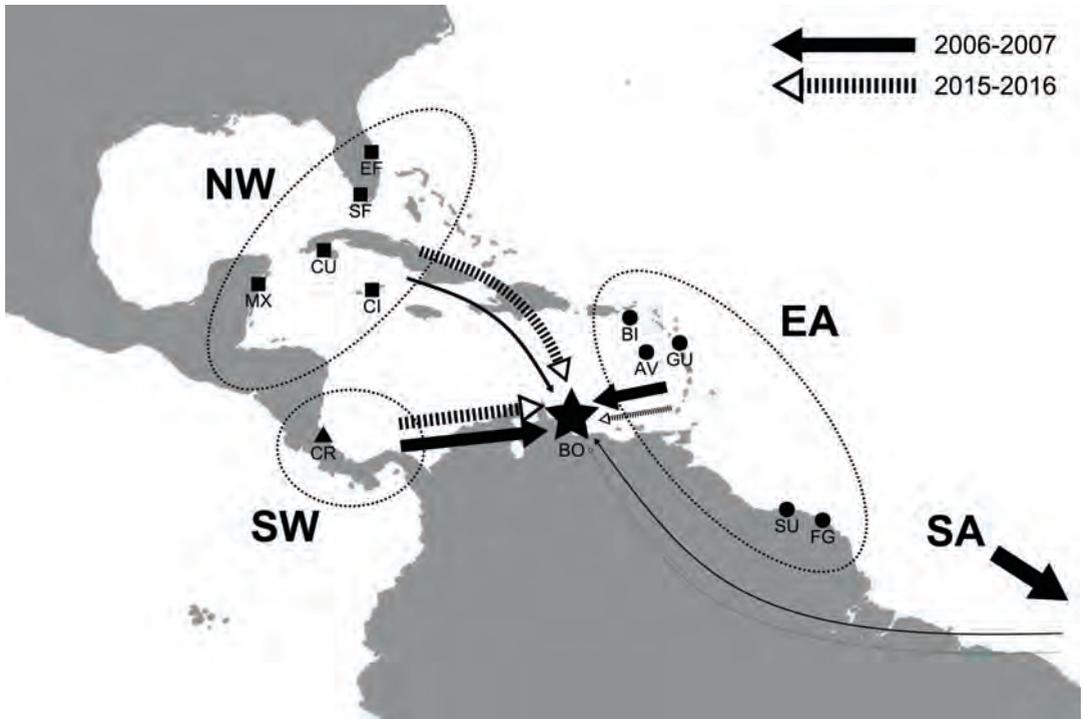


Figure 6.1. The relative amount of juvenile green turtle recruitment from rookeries in the north-western Caribbean (squares; NW), south-western Caribbean (triangle; SW), eastern Caribbean (circles; EA) and southern Atlantic (SA) regions to the Lac Bay feeding ground (star; BO) in 2006-2007 and 2015-2016. Arrow widths are proportional to the relative amount of recruitment. The locations of the following rookeries are shown: Quintana Roo, Mexico (MX), Cuba (CU), Cayman Islands (CI), South Florida, USA (SF), Central Eastern Florida, USA (EF), Tortuguero, Costa Rica (CR), Buck Island, St. Croix, US Virgin Islands (BI), Aves Island, Venezuela (AV), Guadeloupe (GU), Suriname (SU) and French Guiana (FG).

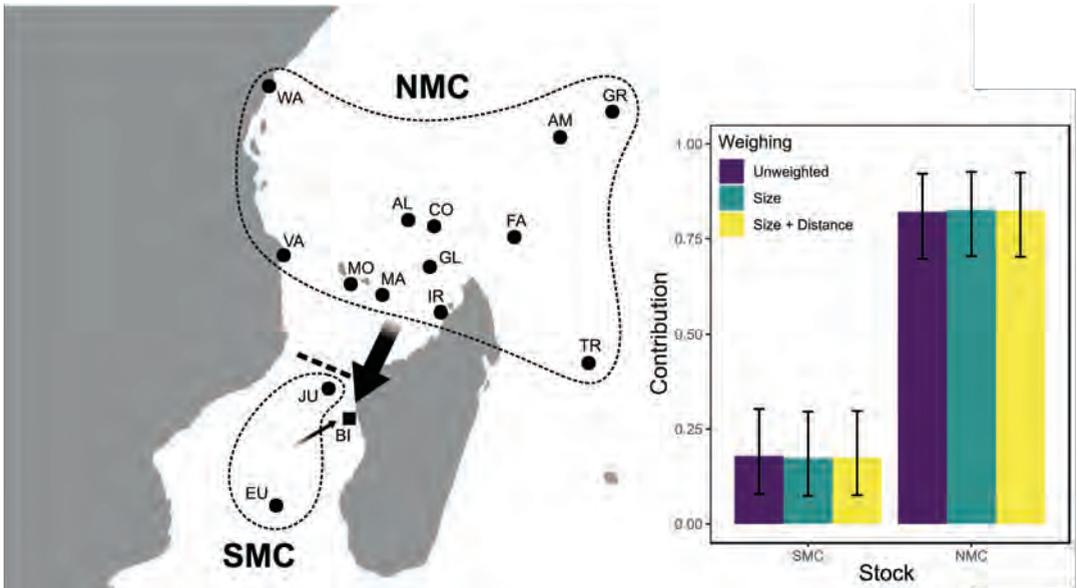


Figure 6.2. The relative amount of juvenile green turtle recruitment from rookeries in the northern (NMC) and southern (SMC) Mozambique Channel stocks to the Barren Isles feeding ground (BI) in 2006-2007. The stock boundary according to Bourjea et al. (2007) is indicated with a thick dashed line. Arrow widths are proportional to the relative amount of recruitment. The locations of the following rookeries are shown: Europa (EU), Juan de Nova (JU), Mayotte (MA), Mohéli (MO), Nosy Iranja (IR), Vamizi (VA), Glorieuses (GL), Cosmoledo (CO), Tromelin (TR), Watamu (WA), Aldabra (AL), Farquhar (FA), Amirantes Group (AM) and Granitic Group (GR).

Differences in the relative contributions from Caribbean rookeries to the Lac Bay feeding ground showed a temporal shift between the periods 2006-2007 and 2015-2016; recruitment from eastern Caribbean rookeries decreased while recruitment from northwestern Caribbean rookeries increased (Fig. 6.1). The changes in relative contribution correlated with population recovery trends in the Caribbean; northwestern Caribbean rookeries showed the relative highest amount of recovery, whereas eastern Caribbean rookeries the lowest. These findings supported the hypothesis that demographic changes, i.e. population recovery assessed via nesting trends, at rookeries can affect recruitment of juveniles to feeding grounds. Furthermore, the findings of Chapter 2 demonstrated that genetic monitoring can be a powerful tool for assessing meta-population dynamics in sea turtles.

Ocean currents strongly influence juvenile sea turtle dispersal in the Southwest Indian Ocean

Chapter 3 described an assessment of juvenile recruitment to a Southwest Indian Ocean green turtle feeding ground located in the Barren Isles of the coast of Madagascar in the southern Mozambique Channel. The aim was to investigate the impact of ocean currents on juvenile dispersal in sea turtles. Recruitment from green turtle rookeries in the southern Mozambique Channel was low, while recruitment from northern Mozambique Channel rookeries was high (Fig. 6.2). The findings of Chapter 3 were consistent with southward dispersal of juvenile green turtles in a general southward flow of ocean currents through the Mozambique Channel and supported an important role for ocean currents in sea turtle juvenile dispersal. Ocean currents are highly variable and complex in the Mozambique Channel, however, and can possibly result in temporal fluctuations in sea turtle dispersal patterns. Given that the study described in Chapter 3 only comprised samples taken during two consecutive years, reliable assessment of temporal fluctuations in juvenile recruitment to the Barren Isles feeding ground was not possible. Genetic monitoring at feeding grounds for prolonged periods of time will be required to assess whether recruitment dynamics are also highly variable.

Pre-glacial origins, glacial isolation and post-glacial admixture characterize the phylogeographic history of green turtles in the Atlantic and Southwest Indian Ocean

Chapter 4 showed the results of a study on the population structure and phylogeography of green turtles in the Atlantic and Southwest Indian Ocean using double digest restriction site associated DNA sequencing. Coalescent model selection supported a scenario where the Caribbean and Southwest Indian Ocean populations diverged from the East Atlantic population. Divergences time estimates were associated with the timing of the last interglacial period (130 – 116 thousand years ago; kya) and the early stage of the previous glacial period (116 – 90 kya). Analysis of genetic diversity and structure among the Caribbean, Southeast Atlantic and Southwest Indian Ocean revealed a pattern of admixture and secondary contact in the two peripheral regions, i.e., the Caribbean and Southwest Indian Ocean. The presence of three distinct genetic clusters associated with the Caribbean, East Atlantic and Southwest Indian Ocean suggested green turtles became isolated in three glacial

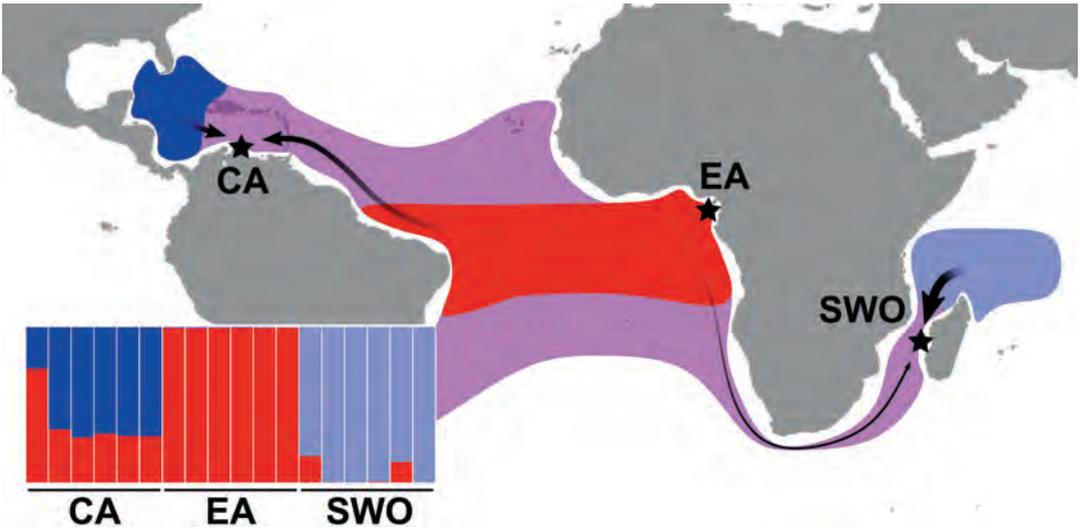


Figure 6.3. The phylogeographic history of green turtles in the Atlantic and Southwest Indian Ocean based upon the findings in Chapter 4 and previous studies. The hypothetical distribution of an ancestral population that existed during the last interglacial (130 – 116 thousand years ago) is shown in purple. The three refugial populations are color-coded according to the admixture proportions estimated using model-based clustering (bottom-left insert). Arrows indicate post-glacial expansion and colonization pathways. Stars denote the sampling site locations of Chapter 4: Caribbean (CA), East Atlantic (EA), Southwest Indian Ocean (SWO).

refugia. The last most recent common ancestor to Atlantic and Southwest Indian Ocean green turtles was dated back to the relatively warm last interglacial period (130 – 116 kya). The findings of Chapter 4 suggest that the onset of the last glaciation (116 – 14 kya) first resulted in 1) isolation among Atlantic and Southwest Indian Ocean green turtles and later 2) isolation among Caribbean and South Atlantic green turtles. After the termination of the last glaciation, the three populations isolated in glacial refugia expanded and admixed in the Caribbean and Southwest Indian Ocean (Fig. 6.3).

Shallow marine habitat area severely declined during the last glacial period and had major impacts on the past population dynamics of hawksbill turtles

In Chapter 5, past changes in the genetic diversity of hawksbill turtles in the Caribbean were investigated, in relation to fluctuations in shallow marine habitat area as a result of sea level changes driven by the Pleistocene glacial cycles. Chapter 5

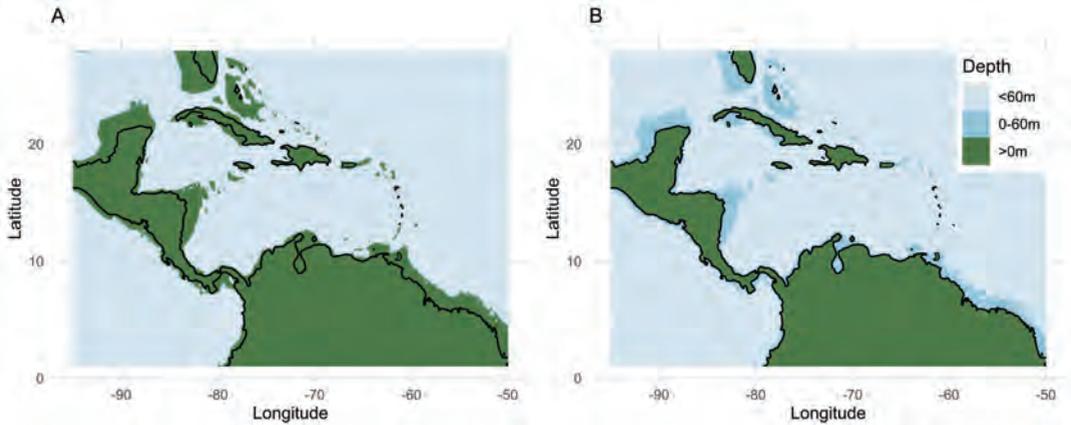


Figure 6.4. The distribution of landmass (>0m depth), shallow marine habitat (0 – 60m depth) and deeper marine habitat (<60m depth) in the Caribbean during the A) Last Glacial Maximum and B) present. Present-day major coastlines in the Caribbean are highlighted with a black line.

demonstrated that shallow marine habitat area, defined as marine habitat between 0 and 60 meters deep, was severely reduced throughout the last glacial period (Fig. 6.4). Relatively minor decreases in sea levels resulted in considerable declines in shallow marine habitat area (Fig. 6.5A). Past changes in shallow marine habitat area (Fig. 6.5B) correlated strongly with past changes in genetic diversity (Fig. 6.5C). Genetic diversity showed a gradual decline during the last glacial period (116 – 14 kya) and

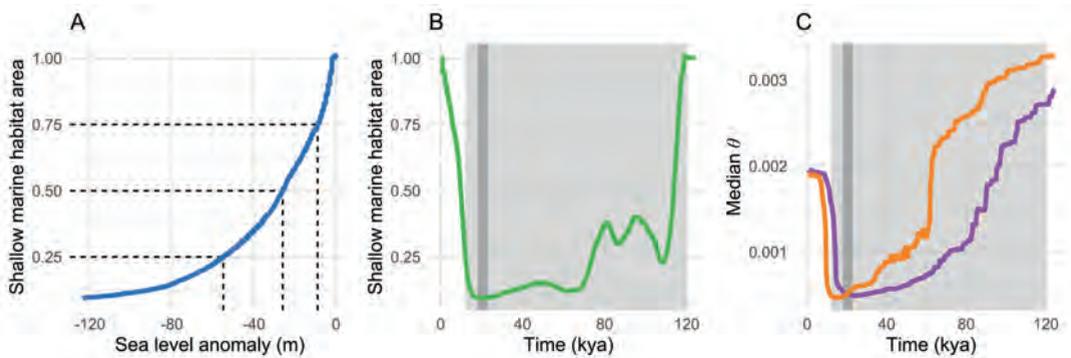


Figure 6.5. The A) amount of shallow (0 – 60m deep) marine habitat area (relative to the present) versus the sea level anomaly. The dashed a reduction in shallow habitat area to 0.75, 0.50 and 0.25 of present-day levels is achieved at sea levels that are 9m, 26m and 55m lower than contemporary sea levels. Changes in B) shallow habitat area and C) median genetic diversity (θ) for mutation rates of $= 7.9 \times 10^{-9}$ (purple) and $= 1.2 \times 10^{-8}$ (orange) substitutions per site per generation during the last 125 thousand years.

decreased to 25% of present-day genetic diversity during the Last Glacial Maximum (26 – 19 kya). After the onset of the current interglacial approximately 14 kya, genetic diversity increased sharply and suggested Caribbean hawksbill turtles experienced a rapid population expansion as global climate conditions warmed, continental ice sheets regressed and sea levels rose. Hawksbill turtles are closely associated with coral reef habitat typically found in shallow waters. The loss of shallow marine habitat likely affected hawksbill turtle population dynamics through bottom-up processes, suggesting past sea level changes affected feeding habitat availability. These findings have broad significance for our understanding of the impact of past climate change and sea level fluctuations on tropical coastal ecosystems.

Concluding remarks

The contemporary genetic diversity and structure of sea turtle populations was shaped by an interplay of intrinsic and extrinsic processes. In the present thesis, I investigated the ecology and evolution of sea turtles using genetic approaches. Chapters 2 highlighted the potential for genetic monitoring as a tool for assessing changes in recruitment dynamics and meta-population dynamics through time in sea turtles. This was underlined in Chapter 3, where a limited temporal sample precluded investigating whether juvenile sea turtle recruitment dynamics changed through time. Tracking the migrations of marine species is often a challenging enterprise, and linking the dynamics of marine populations across the seascape perhaps represents an even greater challenge due to the many factors influencing dispersal in marine species. Linking population dynamics throughout the marine realm can benefit our understanding of the meta-population ecology of marine species and can potentially greatly contribute to marine conservation and management. However, resolving the migratory connectivity among different regions is critical to assessing meta-population dynamics, which requires fine-scale identification of population structure. The identification of population structure represents a challenge when genetic approaches are employed and genetic differentiation among populations is limited, as is common in the marine realm. Advances in DNA sequencing technologies greatly improve our ability to cost-effectively characterize genetic variation throughout the genome and holds great promise for studying the population structure and phylogeography of natural populations. In Chapters 4 and 5, large numbers of genome-wide single nucleotide polymorphism (SNP) markers were used to study

population structure and phylogeography in sea turtles and provided novel insights in our understanding of the evolutionary history of sea turtles. Furthermore, the genomic data generated in these Chapters can represent a valuable genomic resource for sea turtle researchers and conservationists worldwide. However, expanding the number of genetic markers is no panacea. Fundamental discussions about what a population is, and more practical discussions regarding at which level of genetic differentiation populations should be assigned to separate management units, are warranted as well. Integrative and trans-disciplinary approaches, such as those applied in Chapter 5, will be required that combine empirical molecular ecology, theoretical and statistical population genetics, habitat suitability modeling, biogeography and paleontology to reconstruct past ecosystems and deepen our understanding of the structure and diversity of natural populations marine phylogeography.

