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### Evolutionary ecology of sea turtles

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# Summary

## Summary

The genetic diversity and structure of natural populations is the product of past and present ecological and evolutionary processes, which can be intrinsic, such as behavioural or ecological factors, or extrinsic, such as environmental variation and climate change. Molecular markers can be used to study the genetic diversity and structure of natural populations to gain a fundamental understanding of the extrinsic and intrinsic processes that underlie their evolutionary histories. These insights are critical to understanding the ecology and evolution of species, and can play significant roles in aiding conservation and management.

In the present doctoral thesis, traditional and next-generation DNA sequencing approaches were employed to investigate the intrinsic and extrinsic processes that shaped the genetic diversity and structure of the green turtle, *Chelonia mydas*, and hawksbill turtle, *Eretmochelys imbricata*, in the Atlantic and Southwest Indian Ocean. The thesis was divided into two sections: an ecological section (Chapters 2 and 3) concerned with the intrinsic and extrinsic processes affecting dispersal and recruitment dynamics in sea turtles in the present and an evolutionary section (Chapters 4 and 5) that addressed questions regarding the influence of past climate and environmental change on the evolution of sea turtles.

In Chapter 2, the effect of changes in population dynamics at rookeries on juvenile recruitment to feeding grounds was investigated by monitoring temporal changes in the genetic composition at a major juvenile green turtle feeding ground in the southern Caribbean using mitochondrial DNA control region sequences. Temporal changes in the frequencies of mitochondrial DNA haplotypes indicated recruitment from eastern Caribbean rookeries decreased between 2006 and 2016, whereas recruitment from northwestern Caribbean rookeries increased during this period. Changes in recruitment through time correlated with population recovery trends in the Caribbean; northwestern Caribbean rookeries showed the highest degree of recovery, whereas the lowest degree of recovery was observed in eastern Caribbean rookeries. These findings suggested that changes in population dynamics at rookeries can affect recruitment of juveniles to feeding grounds and can influence sea turtle meta-population dynamics.

In Chapter 3, mitochondrial DNA control region sequences were used to investigate the influence of ocean currents on juvenile dispersal in green turtles in the Southwest Indian Ocean. Recruitment from northern Mozambique Channel rookeries to a juvenile green turtle feeding ground located in the southern Mozambique Channel

was high, while recruitment from southern Mozambique Channel rookeries was low. The relatively high recruitment from northern rookeries to a juvenile feeding ground located in the southern Mozambique Channel supported a scenario where juvenile green turtle dispersal was mediated by southward flowing ocean currents. These findings suggested an important role for ocean currents in determining juvenile sea turtle dispersal patterns, though more long-term studies are needed to further investigate the temporal stability of juvenile recruitment patterns in the face of the complex and variable oceanography of the Southwest Indian Ocean.

In Chapter 4, the influence of past climate and environmental change on the population structure and phylogeography of green turtles was studied in the Atlantic and Southwest Indian Ocean. A large number of single nucleotide polymorphisms (SNPs) were obtained from green turtles sampled in the East Caribbean, the East Atlantic and the Southwest Indian Ocean using double-digested restriction site associated DNA sequencing. Model-based clustering supported the presence of three genetic clusters and revealed signatures of admixture in the East Caribbean and Southwest Indian Ocean. The last most recent common ancestor of Atlantic and Southwest Indian Ocean green turtles in the was dated to the last interglacial period (130 – 116 thousand years ago), which was a relatively warm period. The divergence of Southwest Indian Ocean and East Caribbean green turtles from the East Atlantic population was associated with the transition from the last interglacial period (130 – 116 thousand years ago) to the last glacial period (116 – 14 thousand years ago). The findings of Chapter 4 suggested that ancestral Atlantic and Southwest Indian Ocean green turtles became isolated in three glacial refugia during the last glaciation, and subsequently expanded and admixed in the East Caribbean and Southwest Indian Ocean after the termination of the last glacial period approximately 14 thousand years ago.

In Chapter 5, the impact of past sea level fluctuations on the evolution of sea turtles was investigated in Caribbean hawksbill turtles using a modified approach to double-digested restriction site associated DNA sequencing to account for potential biases caused by PCR enrichment. Past fluctuations in genetic diversity were estimated from the folded site frequency spectrum and correlated with changes in shallow marine habitat area, i.e. habitat with a depth between 0 and 60 meters, during the last 125 thousand years. The findings of Chapter 5 showed that shallow marine habitat area was severely reduced throughout the last glacial period. Furthermore,

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past changes in shallow marine habitat area correlated strongly with past changes in genetic diversity. Genetic diversity increased sharply after the end of the last glaciation, suggesting Caribbean hawksbill turtles rapidly expanded as global climate conditions warmed, continental ice sheets regressed and sea levels rose. The findings of Chapter 5 demonstrated past sea level fluctuations had a strong impact on the past population dynamics of hawksbill turtles in the Caribbean, possibly through reduced feeding habitat availability during periods with lower sea levels.







# Samenvatting

De genetische diversiteit en structuur van wilde populaties is het product van historische en hedendaagse ecologische en evolutionaire processen. Deze processen kunnen intrinsiek, zoals gedrag of ecologische factoren, of extrinsiek, zoals bijvoorbeeld variatie in omgevingsfactoren en klimaatverandering, zijn. Moleculaire merkers kunnen gebruikt worden om de genetische diversiteit en structuur van wilde populaties te bestuderen en zo een fundamenteel inzicht in de intrinsieke en extrinsieke processen die ten grondslag liggen aan hun evolutionaire historie te verkrijgen. Deze inzichten zijn van kritiek belang voor het begrijpen van de ecologie en evolutie van soorten en kunnen een belangrijke rol spelen in natuurbescherming.

In dit proefschrift zijn vraagstukken onderzocht met betrekking tot de intrinsieke en extrinsieke processen die ten grondslag liggen aan de genetische diversiteit en structuur in de groene zeeschildpad, *Chelonia mydas*, en karetschildpad, *Eretmochelys imbricata*, in de Atlantische en Zuidwest-Indische Oceaan. Hierbij is gebruik gemaakt van zowel traditionele methoden voor de sequentiëring van DNA als *next generation sequencing*. Het proefschrift bestaat uit twee delen: een ecologisch deel (Hoofdstukken 2 en 3) en een evolutionair deel (Hoofdstukken 4 en 5). Het ecologische deel heeft betrekking tot de intrinsieke en extrinsieke processen die van invloed zijn op de hedendaagse dispersie-, en rekruteringsdynamiek van zeeschildpadden. Het evolutionair deel behandelt vraagstukken over de invloed van historische klimaat-, en omgevingsveranderingen op de evolutie van zeeschildpadden.

In Hoofdstuk 2 is onderzoek gedaan naar de invloed van veranderingen in populatiedynamiek in broedkolonies op de juveniele rekrutering naar voedingsgronden. Hiervoor werden veranderingen over tijd in de genetische samenstelling van een populatie juveniele groene zeeschildpadden in een belangrijke voedingsgrond in de zuidelijke Cariben gedurende tien jaar geobserveerd met behulp van mitochondriaal DNA. Veranderingen over tijd in frequenties van mitochondriale DNA haplotypen lieten zien dat de proportie juvenielen afkomstig uit broedkolonies in de oostelijke Cariben afnam tussen 2006 en 2016, terwijl de proportie juvenielen afkomstig uit de noordwestelijke Cariben toenam in deze periode. De veranderingen over tijd in rekrutering waren gecorreleerd met populatietrends in de Cariben; broedkolonies in de noordwestelijke Cariben lieten de hoogste mate van populatieherstel zien, terwijl de laagste mate van populatieherstel geobserveerd werd in broedkolonies in de oostelijke Cariben. Deze bevindingen suggereerden dat

veranderingen in de populatiedynamiek in broedkolonies van invloed kunnen zijn op de rekrutering van juvenielen naar voedingsgronden en een belangrijke rol kunnen spelen in de meta-populatiedynamiek van zeeschildpadden.

In Hoofdstuk 3 werd de invloed van zeestromen op de dispersie van juveniele zeeschildpadden onderzocht in de Zuidwest-Indische Oceaan met behulp van mitochondriaal DNA. De rekrutering van juveniele groene zeeschildpadden afkomstig uit broedkolonies in het noordelijke deel van de Straat Mozambique naar een voedingsgrond gelokaliseerd in het zuidelijke deel van de Straat Mozambique was hoog, terwijl de rekrutering van juvenielen afkomstig uit zuidelijke broedkolonies laag was. Het relatief hoge aantal juvenielen afkomstig uit noordelijke broedkolonies in een zuidelijke voedingsgrond was consistent met dispersie in zuidwaartse zeestromen in de Straat Mozambique. Deze bevindingen ondersteunen een belangrijke rol voor zeestromen in het bepalen van dispersiepatronen in juveniele zeeschildpadden, hoewel er meer lange-termijn studies nodig zijn naar de stabiliteit van juveniele dispersiepatronen door tijd gezien de complexe en variabele oceanografische kenmerken van de Zuidwest-Indische Oceaan.

In Hoofdstuk 4 werd de invloed van klimaat-, en omgevingsverandering in het verleden op de populatiestructuur en phylogeografie van groene zeeschildpadden in de Atlantische en Zuidwest-Indische Oceaan onderzocht. Voor deze studie werd een groot aantal enkel-nucleotide polymorfismen (ook wel *single nucleotide polymorphisms*; SNPs) gekarakteriseerd door middel van *double-digested restriction site associated DNA sequencing* in groene zeeschildpadden uit de Oost-Cariben, Oost-Atlantische Oceaan en Zuidwest-Indische Oceaan. Een modelgebaseerde clusteranalyse ondersteunde de aanwezigheid van drie genetische clusters en demonstreerde tekenen van genetische vermenging en secundair contact in de Oost-Cariben en Zuidwest-Indische Oceaan. De meest recente gemeenschappelijke voorouder van Atlantische-, en Zuidwest-Indische groene zeeschildpadden werd gedateerd tijdens het vorige interglaciaal (130 tot 116 duizend jaar geleden), wat een relatief warme periode was. De afsplitsing van groene zeeschildpadden in de Zuidwest-Indische Oceaan en de Oost-Cariben werd gedateerd rond de overgang van het vorige interglaciaal (130 tot 116 duizend jaar geleden) naar de vorige ijstijd (116 tot 14 duizend jaar geleden). De bevindingen in Hoofdstuk 4 suggereerden dat de voorouders van Atlantische en Zuidwest-Indische groene zeeschildpadden geïsoleerd raakten in drie refugia tijdens de vorige ijstijd, en na het einde van de vorige ijstijd,

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circa 14 duizend jaar geleden, weer met elkaar in contact kwamen in de Oost-Cariben en Zuidwest-Indische Oceaan.

In Hoofdstuk 5 werd de impact van historische zeespiegelveranderingen op de evolutie van zeeschildpadden onderzocht in Caribische karetschildpadden met behulp van een aangepaste *double-digested restriction site associated DNA sequencing* methode om rekening te houden met potentiële statistische afwijkingen veroorzaakt door PCR-verrijking. Historische fluctuaties in genetische diversiteit werden bepaald aan de hand van het gevouwen allelfrequentiespectrum en gecorreleerd met het oppervlakte aan ondiep marien habitat, dat wil zeggen marien habitat met een diepte tussen 0 en 60 meter, gedurende de laatste 125 duizend jaar. De bevindingen in Hoofdstuk 5 lieten zien dat het oppervlakte van ondiepe mariene habitat sterk was gereduceerd tijdens de laatste ijstijd. De historische veranderingen in het oppervlakte van ondiep marien habitat correleerden sterk met historische veranderingen in genetische diversiteit. De genetische diversiteit nam sterk toe na het einde van de laatste ijstijd, wat suggereerde dat Caribische karetschildpadden zeer snel in aantal toenamen nadat het klimaat opwarmde, continentale ijskappen verdwenen en zeespiegels stegen. De bevindingen in Hoofdstuk 5 demonstreerden een sterke invloed van zeespiegelveranderingen op de historische populatiedynamiek van Caribische karetschildpadden, mogelijk omdat de hoeveelheid beschikbare foerageerhabitat afnam tijdens periodes met lagere zeespiegels.





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part of my life. I'd also like to thank my parents, Pieter and Margriet, and sister, Iris, for your love and support, and keeping my feet on *terra firma* when I again spent too much time in the ivory tower. It's reassuring to know that you're always there for me, and are proud of me no matter what. Thank you! A special thanks to my young nephew, Jelte, for bringing a smile to my face and helping me remember what's it all about in the end. I love how you are turning into a little scientist yourself, with seemingly limitless enthusiasm. The thought that you will maybe read this thesis in 20 years from now fills me with so much joy. I also want to thank Henk and Tineke, Amarins and Oeds, and Welmoed and André for all the fun times and really making me feel part the Mous family during these last few years. Sometimes chaotic, always pleasant. Thanks for having me!

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# Dankwoord

## Dankwoord

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# About the author



## About the author



Jurjan Pieter van der Zee was born on June 12<sup>th</sup>, 1990, in Friesland, a province in the northern Netherlands. He became fascinated by natural history during his early childhood, showing great interest in dinosaurs, whales, volcanoes and space. In 2008, he began studying Life Science and Technology at the University of Groningen and majored in Marine Biology, with a minor in Medical Biology, and Behavior and Neurobiology. During his bachelor, he developed an interest in genetics, working on identifying DNA methyltransferase genes in the genome of *Nasonia vitripennis* at the department of Evolutionary Genetics and inferring the population structure of North Atlantic common minke whales, *Balaenoptera acutorostrata*, at the department of

Marine Evolution and Conservation. He earned his bachelor degree in Marine Biology at the University of Groningen in 2012, where he continued his studies to pursue a master's degree in Marine Biology. He worked on the demographic history of several Arctic marine mammals, including polar bears (*Ursus maritimus*), bearded seals (*Erignathus barbatus*) and ringed seals (*Pusa hispida*), with Prof. Dr. Per J. Palsbøll and Dr. Andrea A. Cabrera for his first master project at the department of Marine Conservation and Evolution. For his second master project, he spent several months at the University of Washington in Seattle, United States, working with Prof. Dr. André E. Punt. Here, he applied demographic simulations to assess critical dispersal rates in North Atlantic common minke whales, and used genetic simulations to evaluate whether genetic methods would be able to detect structure at the inferred critical dispersal rates. The experiences he had during his master helped him discover his inner computer nerd, developing a passion for programming. He obtained his master's degree in Marine Biology from the University of Groningen in 2015 and that same year started his PhD with Prof. Dr. Per J. Palsbøll, where he worked on the population structure, migration patterns and demographic history of green turtles, *Chelonia mydas*, and hawksbill turtles, *Eretmochelys imbricata*. In his spare time, he enjoys reading fantasy novels, cooking and barbecuing, and is a boardgame enthusiast. He is also an avid musician, enjoying guitar, piano and drums, and has played guitar in several bands, with which he participated in band contests, recorded a few songs and played live on the local radio.