GENETIC DIVERSITY, CONNECTIVITY AND DEMOGRAPHIC HISTORY OF BONAIRE SEA TURTLES

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with a discussion on sampling mixed aggregations for demographic inferences

SECOND MASTER RESEARCH PROJECT

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ABSTRACT

Climate change is threatening sea turtles globally, and whether or not sea turtles will be able to adapt to and survive global warming may depend in part on their genetic diversity. Sea turtles have survived several past environmental changes, but these events, together with the more recent human exploitation, might have substantially decreased sea turtle genetic diversity.
In the present study, we investigated the green sea turtles of the feeding aggregation off Bonaire in the Dutch Caribbean for their genetic diversity, demographic history, and connectivity to other Caribbean and Atlantic feeding aggregations and rookeries.
We found current nucleotide diversity to be the highest among all Caribbean and Atlantic feeding aggregations and rookeries included in this study, while haplotype diversity was intermediate. The inferred demographic history showed a possible slight decline in genetic diversity during the past 6,000 years. The Bonaire feeding aggregation was significantly genetically differentiated from all but two other Caribbean and Atlantic feeding aggregations and rookeries, highlighting Bonaire's uniqueness and the importance of its conservation.
However, since sea turtle feeding aggregations comprise sea turtles from several genetically distinct rookeries, we hypothesized that the demographic history inferred for Bonaire might not display local, but rather "imported" patterns from the main contributory rookeries.
A comparison between the Bonaire feeding aggregation's demographic history and the main contributory rookeries' supports this hypothesis. Hence we discuss the implications of sampling mixed (sea turtle) feeding aggregations on population demographic inferences in a wider context and propose future research, management and conservation strategies.
We additionally found that historic environmental changes (such as the Last Glacial Maximum) do not seem to have been associated with decreases in sea turtle genetic diversity in all but one main contributory rookery. This suggests that green sea turtle genetic diversity may not have been eroded strongly by past climatic events and may serve as "buffer" against at least some future changes.

INTRODUCTION

Climate change is threatening sea turtles globally (e.g., Fuentes et al. 2013, Hawkes et al. 2009, Tomillo et al. 2015). As very old species (Bowen and Karl 2007), sea turtles have survived several past environmental changes. However, it is uncertain if these past events have decreased the genetic diversity of sea turtles, and if so, to what extent. It also remains unclear if the more recent, often extensive human exploitation has worsened the effect (Jackson et al. 2001, Parsons 1962). Given that there is a larger probability that a species or population adapts to and survives a novel (environmental) change or stressor if its genetic diversity is large (described in Schindler et al. 2010 as "portfolio effect"; compare also Lande and Shannon, 1996, Booy et al. 2000), understanding the current level of genetic diversity as well as its divergence from the level of genetic diversity that had enabled the survival of past changes, becomes important for conservation efforts.
Current developments within the areas of coalescent theory and Bayesian inference have improved the reconstruction of a species' or population's demographic history (i.e., past genetic diversity over time, estimated as theta, θ (the product of effective breeding population size, N_{ef}, and generation length, τ)) based on current molecular data (Drummond et al. 2005, Ho and Shapiro 2011, Minin et al. 2008).
We applied these methods to the green sea turtle feeding aggregation around Bonaire, which is

one of the largest aggregations in Dutch Caribbean waters, yet poorly studied in terms of genetic diversity, connectivity and demographic history. Accordingly, the first aim of this study was to investigate the current genetic diversity of the green sea turtles feeding around Bonaire, to investigate how connected or unique the Bonaire feeding aggregation is compared to other Caribbean and Atlantic feeding aggregations and rookeries, and to reconstruct the demographic history.

However, since sea turtle feeding aggregations are known to be composed of individuals originating from different, genetically structured rookeries (review by Bowen and Karl 2007; for green sea turtles: e.g., Bass et al. 1998, Bass et al. 2006, Lahanas et al. 1998, Luke et al. 2004, Naro-Maciel et al. 2007), we were also interested in whether the demographic history we reconstructed really represented the past genetic diversity of the green sea turtles feeding aggregation of Bonaire, or whether the demographic history was "imported" from the (main) rookeries of origin.

Therefore, the second aim of this study was to investigate the demographic histories of the rookeries that contribute most sea turtles to the Bonaire feeding aggregation, and to compare these demographic histories with the one inferred for Bonaire.

From this comparison, we discuss implementations of sampling mixed aggregations for demographic inferences and for conclusions drawn from those inferences.

Finally, we discuss our findings in the context of conservation and management of the Bonaire feeding aggregation, especially in the light of the recently emerging discussions about reassuming sea turtle fisheries (Sea Turtle Conservation Bonaire, pers. com.).

Feeding aggregation
Mixed stock of sea turtles; where the sea turtles forage, mature and spend the vast majority of their life (e.g., Bowen et al. 2007, Bowen and Karl 2007)

Rookery
Place and (sub)population of origin; where the sea turtles had hatched and where they return to to breed in intervals of approximately 2 to 3 years once they've reached maturity (e.g., Bowen and Karl 2007, Norman et al. 1994, Dethmers et al. 2006)

MATERIAL & METHODS

Bonaire data - field sampling

Tissue samples were collected from juvenile green sea turtles caught by scuba/snorkelling assisted hand-capture or using netting techniques during in-water surveys (1) in or (2) outside Lac Bay or (3) around Klein Bonaire, Bonaire, Dutch Caribbean (see *Figure 1*). Samples span from the year 2010 (n=34 sea turtles) to 2012 (n=6 sea turtles in 2011 and n=1 sea turtle in 2012) and were collected at four different time points each year (March (only samples from 2011), May (samples from 2010 and 2011), October (sample from 2012) and December (samples from 2010)).

Samples were either taken with a biopsy punch (6mm, Miltex®) or a scalpel in the neck or from the front flipper of the sea turtle. Samples were stored in 25% dimethylsulfoxide (DMSO) or 70% ethanol and preserved in a fridge at -4 degrees C. Upon transfer to the laboratory at the University of Groningen, samples were preserved at -20 degrees C for short term storage and -80 degrees C for long term storage.

Molecular analyses

DNA was extracted from the tissue samples using the Gentra Puregene® Core Kit A, following the Qiagen® extraction protocol: Approximately 10 to 25 mg of each sample was cut into small
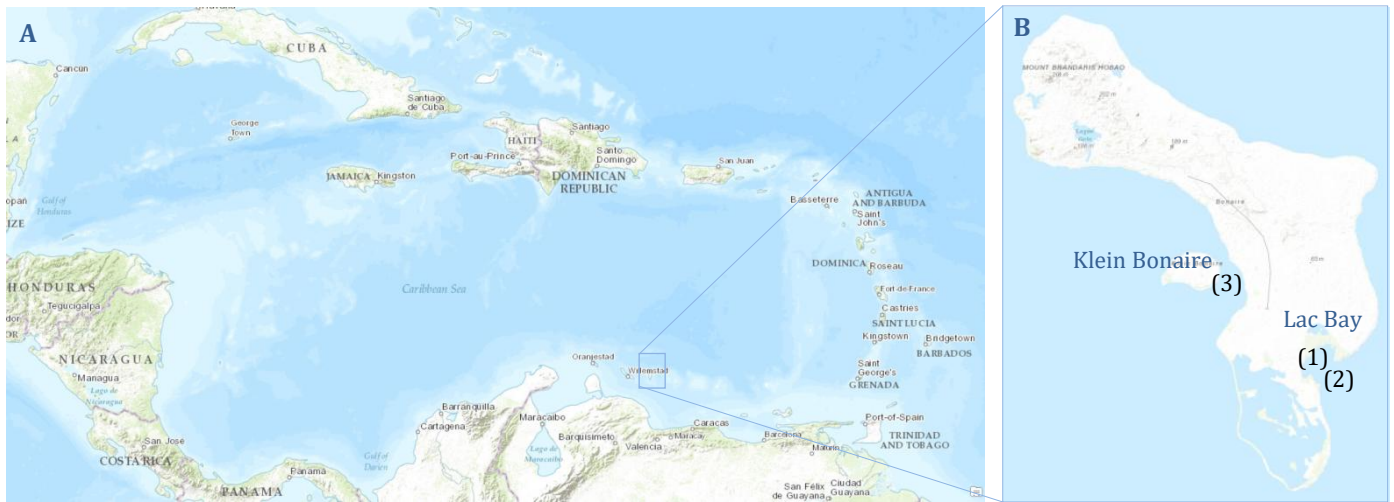
FIGURE 1 Location of the Bonaire sea turtle feeding aggregation. **A** The location of the Bonaire green sea turtle feeding aggregation within the Caribbean region. **B** The location of the three sampling sites Lac Bay (1), outside Lac Bay (2), and around Klein Bonaire (C). Maps have been generated in *Arc*GIS (® Esri).

pieces using sterilized forceps and scalpels. 300 µl of Cell Lysis Solution was then added to the samples before homogenization through vortexing. Subsequently, we added 1.5 µl of Proteinase K, mixed the sample by inverting and incubated them overnight in a heat block set to 55 degree C. After incubation, 100 µl of Protein Precipitation Solution was added before vortexing for 20 seconds. We then centrifuged the samples for 3 minutes at 13000*g and poured the supernatant of each sample into 300 µl of isopropanol in fresh sterile microcentrifuge tubes. The new tubes were inverted gently 20 to 30 times, then centrifuged again for 1 minute at 13000*g. The supernatant was carefully discarded by inverting the tubes onto absorbent paper. The pellet remained in the tube was washed by adding 300 µl of 70% ethanol and inverting the tube several times. After centrifugation for 1 minute at 13,000 x g, the resulting supernatant was discarded onto absorbent paper and any remaining ethanol residues removed by pipette after brief vortexing. To ensure all ethanol was removed, samples were allowed to air-dry for minimally 15 minutes. Then, 50 µl DNA Hydration Solution was added to the pellets and samples were mixed by flicking a few times. The samples were then incubated at 65 degrees C for one hour to ensure the DNA could dissolve, and further incubated at room temperature over night. DNA quantity obtained from each extraction was assessed by fluorometric quantitation following the Qubit® protocol: A Qubit™ working solution was produced mixing 1*(number of samples+2) µl Qubit™ reagent and 199*(number of samples +2) µl Qubit™ Buffer. From this working solution, 190 µl were used for each of the two standard sample used to calibrate the Qubit® 2.0 Fluorometer measurements. To both tubes of 190µl working solution, 10 µl of each standard (part of the Qubit™ kit) was added. From the remaining working solution, 199 µl per extracted DNA sample were transferred into clean centrifuge tubes. 1 µl of each extracted DNA sample was then added to a single working-solution tube. After 2 minutes of incubation at room temperature in the dark, we used the standards to calibrate the Qubit® 2.0 Fluorometer (molecular probes™, invitrogen™) and subsequently measured DNA quantity [ng/µl] in our samples.

Before amplifying the mtDNA control region, a master mix of 1µl Taq™-buffer, 4µl dGATC-mix (0.5µM per nucleotide;), 1µl of each primer (LCM15392 (forward; 5' GCT TAA CCC TAA AGC ATT GG 3') and H950g (reverse; 5' GTC TCG GAT TTA GGG GTT TG 3'), both at a concentration of 10nM), 2µl of autoclaved MilliQ H_2O and 0.08µl Taq™ DNA polymerase was made. From this master mix, aliquots of 9µl were transferred into fresh tubes and 1µl of our sea turtle DNA was added to each one.

After an initial cycle of 2 minutes at 94 degrees C, amplification conditions of the polymerase

chain reaction (PCR) for the following 32 cycles were: 30 seconds at 94 degrees C (the denaturing temperature), 45 seconds at 52 degrees C (the annealing temperature), and 30 seconds at 72 degrees C (the extension temperature). The closing cycle was 5 minutes at 72 degrees C; then, samples were stored at 10 degrees C until removal.

To check DNA quality through electrophoresis, we run 5µl (10µl of the controls) of each amplification product with 2µl of No. VI loading buffer on a 0.7% Agarose™ gel for 45 minutes at 75V and 500mA. Furthermore, we checked whether the mtDNA fragment we aimed for was present in the amplification products by running 5µl of our amplification products with 2µl of the same loading buffer on a 2% Agarose™ gel, also for 45 minutes, 75V and 500mA.

PCR products that had amplified successfully (shown high DNA quality and the presence of the aimed-for mtDNA sequence on the electrophoresis gel) were purified by having Exonuclease I digest excess PCR primers and Shrimp Alkaline Phosphatase degrade excess nucleotides (SAP-Exo purification protocol).

Cycle-sequencing was conducted after adding 0.5µl Terminator Ready Reaction Mix, Big Dye® version 3.1. (applied Biosystems, P/N 4337455), 1.5µl 5X Big Dye® sequencing buffer (included in the above-mentioned kit), 0.17µl primer (at 10µM) and 2.83µl autoclaved Milli-Q H_2O to every 5µl of clean PCR product. Two different reverse primers targeting the mtDNA control region were used for each individual sea turtle sample: CM16006R (5' AACTACCGTATGCCAGGTTA 3') (designed *in-house*) and H950g (5' GTC TCG GAT TTA GGG GTT TG 3') (Abreu-Grobois et al. 2006), due to mtDNA throughput size restrictions imposed by the capillary length of the sequencing machine.

Amplification conditions were 10 seconds at 96 degree C (denaturing temperature), followed by 5 seconds at 50 degree C (annealing temperature), and 4 minutes at 60 degree C (extension temperature), for 25 cycles.

Following cycle-sequencing, extension products were purified using Ethanol/EDTA precipitation: 60 µl 100% Ethanol and 5 µl 125mM EDTA (previously mixed) were added to each sample well, before the sample plate was covered with a sealing mat and inverted 4 to 10 times to mix. The plate was then incubated for 15 minutes at room temperature to allow precipitation. Subsequently, we centrifuged the samples for 30 minutes at 3000*g and 8 degrees C. After centrifugation, we immediately removed the sealing mat and inverted the sample plate onto absorbent paper in order to remove the supernatant.

Then, 60 µl of 70% Ethanol was added and the samples spun at 1650*g for 15 minutes. After this step, we inverted the plate again immediately onto absorbent paper and, leaving it inverted on fresh absorbent paper, spun the plate again for less than a minute at 250*g in order to completely remove any supernatant residues. We then dried the plate in an oven at 65 degrees C for 8 minutes, and added 10µl of Hi Di Formamide (applied Biosystems, P/N 4311320) to each sample and waited at least 30 minutes to allow the DNA to re-suspension before Sanger sequencing.

Sanger sequencing was then performed in a 3130 DNA Analyser™ machine.

Sequence alignment, truncation and creation of consensus sequences

Chromatograms were inspected visually, reversed, complemented and trimmed in Chromas 2.6 (©Technelysium Pty Ltd). The resulting sequences were aligned using the ClustalW Multiple Alignment algorithm (Thompson et al. 1994) as implemented in MEGA version 7.0.18 (Kumar et al. 2016) with default settings but for the DNA Weight Matrix (set to ClustalW (1.6), but with the standard transition weight of 0.5). Alignments were inspected visually again. From the two adjacent mtDNA regions we sequenced for each individual, the region sequenced using the CM16006R primer was truncated to a characteristic nucleotide repetition (5' AGGAAGAGAAA 3')

at the 3' end. Its 5' end as well as both ends of the sequence captured with the H950G primer were not truncated in order to allow maximum overlap between the two sequenced mtDNA regions. This enabled the creation of consensus sequences for each individual and maximized the consensus sequences' lengths.

Samples that had resulted in poor quality chromatograms (only ambiguous chromatogram peaks or none at all) were re-sequenced if possible or omitted if consistently poor. Ambiguous nucleotides and singleton polymorphic nucleotides were inspected using BioEdit version 7.2.5 (Hall 1999) and corrected if necessary.

Combining the two sequencing products of each individual, we generated one mtDNA control region consensus sequences for each individual, and trimmed them at the 5' end to the shortest sequences (resulting in a length of 824 base pairs) using BioEdit.

Caribbean and Atlantic data

We obtained 75 mitochondrial (mt)DNA control region sequences of Bonaire sea turtles from an earlier study (Velez-Zuazo 2008). Those samples had been collected between 2006 and 2007 using scuba/snorkelling assisted hand-capturing or netting, as described above, on in-water surveys around Bonaire, using a disposable biopsy punch (Acuderm®) and had been stored in either 20% DMSO-20%EDTA or 95% ethanol and preserved at room temperature. DNA had been extracted and sequenced at the Laboratory of Animal Evolutionary Genetics, University of Puerto Rico, Rio Piedras, in 2008 (for protocol compare Velez-Zuazo 2008).

mtDNA haplotype data from other Caribbean as well as Atlantic feeding grounds and rookeries was retrieved from literature (for number and length of sequences, haplotypes and references see *Table 1* and caption). The corresponding nucleotide sequence for each haplotype was either retrieved directly from the below-mentioned literature or from *GenBank* (http://www.ncbi.nlm.nih.gov/genbank/, last accessed 03.09.2016 10:45 a.m.).

We combined the mtDNA sequences generated in the present study with the data from Velez-Zuazo (2008) by truncating our sequences to a length of 482 base pairs and aligning the two data sets in MEGA version 7.0.18 (Kumar et al. 2016), applying the ClustalW Multiple Alignment algorithm (Thompson et al. 1994). The resulting data set will hereafter be referred to as the Bonaire feeding aggregation data set.

We also generated a Caribbean and Atlantic green sea turtle mtDNA data set, aligning the Bonaire feeding aggregation data set with the sequences of the Caribbean and Atlantic feeding aggregations and rookeries in MEGA. We truncated this data set to 486 base pairs, corresponding to the shortest sequence, using MEGA.

TABLE 1 **Haplotype frequencies of Caribbean and Atlantic sea turtle feeding aggregations and rookeries**.

Feeding aggregation or rookery	no of sequences	no of base pairs	Haplotype frequencies (preceded with CM-)
Argentina*	93	491	A5 (20), A6 (2), A8 (59), A9 (5), A10 (1), A24 (1), A32 (2), A39 (1), A42 (2)
Ascension Island	50	497	A6 (3), A8 (43), A24 (1), A39 (1), A45 (1), A46 (1)
Aves Island	30	487	A3 (3), A5 (27)
Bahamas*	79	491	A1 (2), A3 (62), A5 (10), A8 (1), A20 (1), A21 (3)
Barbados*	60	491	A1 (7), A3 (21), A5 (13), A8 (14), A9 (1), A10 (2), A17 (1), A22 (1)
Brazil, Almofala*	117	491	A3 (18), A5 (28), A6 (3), A8 (53), A9 (3), A10 (4), A16 (1), A21 (1), A24 (1), A32 (1), A42 (2), A44 (1), A45 (1)

Brazil, Rocas Atoll	53	491	A8 (36), A9 (7), A10 (2), A11 (1), A12 (5), A26 (1), A32 (1)
Brazil, Ubatuba*	113	491	A3 (2), A5 (14), A8 (83), A9 (4), A10 (3), A24 (2), A32 (2), A44 (1), A46 (1), A55 (1)
Bonaire*	94	491	A1 (2), A2 (1), A3 (40), A5 (39), A6 (1), A8 (4), A17 (2), A20 (1), A21 (1), A22 (1), A29 (1), A47 (1)
Cape Verde*	44	491	A1 (1), A3 (2), A5 (23), A6 (1), A8 (17)
Costa Rica	433	491	A3 (395), A4 (1), A5 (32), A20 (2), A21 (3)
Florida*	62	491	A1 (12), A2 (1), A3 (43), A5 (3), A18 (2), A22 (1)
North Carolina*	106	491	A1 (34), A2 (2), A3 (43), A5 (5), A8 (7), A15 (1), A16 (2), A18 (3), A22 (2), A26 (2), A27 (2), A28 (3)
Suriname	15	491	A5 (13), A6 (1), A7 (1)

Number and haplotype frequencies of green sea turtle mtDNA control region sequences from feeding aggregations (marked by a star) and rookeries (unmarked) in the wider Caribbean and the Atlantic as retrieved from literature. References for the feeding aggregations and rookeries: Argentina (Prosdocimi et al. 2012); Ascension Island (Encalada et al. 1996, Formia et al. 2006); Aves Island (Lahanas et al. 1998); Bahamas (Lahanas et al. 1998); Barbados (Luke et al. 2004); Brazil, Almofala (Naro-Maciel et al. 2007); Brazil, Rocas Atoll (Encalada et al. 1996, Bjorndal et al. 2006) ; Brazil, Ubatuba (Naro-Maciel et al. 2007) ; Bonaire *(from literature)* (Velez-Zuazo 2008); Cape Verde (Monzón-Argüello et al. 2010); Costa Rica (Naro-Maciel et al. 2007, Encalada et al. 1996, Bjorndal et al. 2005); Florida (Bass and Witzell 2000); North Carolina (Bass et al. 2006); and Suriname (Encalada et al. 1996).

Genetic diversity
Genetic diversity was estimated using DNAsp version 5.10.01 (Rozas et al. 2003). For each considered Caribbean and Atlantic feeding aggregation and rookery, we counted the number of haplotypes and number of polymorphic sites, and we estimated haplotype diversity and nucleotide diversity (Nei 1987) excluding sites with missing data or alignment gabs (default in DNAsp). We calculated the Caribbean and Atlantic-wide number of haplotypes and estimated haplotype diversity (combining all feeding aggregations and rookeries) excluding sites with missing data or alignment gaps.

The specific haplotypes of the Bonaire sequences were determined by aligning reference haplotype sequences (of a length of 485 base pairs; as received from the Archie Carr Center for Sea Turtle Research at the University of Florida, http://accstr.ufl.edu/resources/mtdna-sequences/, last accessed: 02.09.2016, 11:00 a.m.) to our sequences in MEGA and generating a haplotype file in DNAsp. Sites with missing data or alignment gaps were excluded for consistency with our genetic diversity estimates. Generating a haplotype file, DNAsp groups the control haplotype sequences together with the corresponding sequences in our data set, revealing the haplotypes and haplotype frequencies within our sample set.

If several reference haplotypes were grouped together (and therefore, our sequences grouped with them could not be attributed unambiguously), the sequences grouped in such "multiple haplotypes-groups" were aligned with longer reference haplotype sequences (800 base pairs) from the same source (the Archie Carr Center for Sea Turtle Research). After alignment and truncation to a total length of 739 base pairs, another haplotype file was generated in DNAsp (not considering sites with missing data or alignment gaps) to revealed which longer reference haplotype our sequences belonged to.

Population structure and connectivity
Genetic differentiation among all Caribbean and Atlantic feeding aggregations and rookeries was calculated as F_{ST} values (Wright 1951) using DNAsp and considering sites with alignment gaps (gaps as the fifth state). We also calculated migration rate, Nm, as number of migrants per

generation between them using Wright's finite island model and equation Nm $\approx \frac{1}{2}(\frac{1}{FST} - 1)$ (Wright 1931).

Differentiation between the Bonaire feeding aggregation and other Caribbean and Atlantic feeding aggregations and rookeries was investigated in DNAsp performing pair-wise Chi square tests on F_{ST} values under exclusion of sites with alignment gaps.

Demographic history of Bonaire sea turtles and main contributor rookeries

Main contributory rookeries

We retrieved information on the composition of the Bonaire feeding aggregation in terms of sea turtle origin from mixed stock analyses in literature (Velez-Zuazo 2008). The five rookeries that study had estimated to contribute the largest numbers of sea turtles to the Bonaire aggregation were Costa Rica (50% of the recruitment), Suriname (30%), Ascension Island (~4%), Aves Island (~4%), and the Rocas Atoll in Brazil (~2%). Hereafter, these five rookeries will be referred to as "main contributory rookeries".

Inference of demographic history

To infer the population demographic history of the Bonaire feeding aggregation as well as of each main contributory rookery, we used Markov Chain Monte Carlo (MCMC) sampling procedure (Drummond et al. 2002) as implemented in BEAST2 (Bouckaert et al. 2014). We run both, a Coalescent Bayesian Skyline (BS) (Minin et al. 2008) and a Coalescent Constant Population (CP) model for the Bonaire feeding aggregation as well as for each main contributory rookery. The Coalescent CP model thereby served as our null hypothesis, against which the Coalescent BS model was tested (using Bayes factors, see below).

Combination of main contributory rookeries

To compare the demographic history inferred for Bonaire not only to the demographic histories of the single contributory rookeries but also to their "combination" into a theoretical migration pool (and to thereby highlight a possible consistency in inferred thetas), we inferred demographic history also for the combination of all main contributory rookeries. To enable the comparison, we used the same prior settings for the BEAST2 run as for the Bonaire feeding aggregation and contributory rookeries (*Table 2*) and did not augment iteration steps above 100,000,000, even though estimated sample sizes were relatively low (i.e., 86.1 and 86.2 instead of at or above 200 for the prior and posterior distribution, respectively).

Nucleotide substitution model

The nucleotide substitution model was determined using jModelTest version 2.1.10. (Darriba et al. 2012) and standard settings (exploring 3 substitution schemes, including models with equal/unequal base frequencies, with/without a proportion of invariant sites, and with/without rate variation among sites, K defined as substitution parameters + 1513 branch lengths + topology, base tree for likelihood calculations set to ML tree, and tree topology search operation set to NNI). The resulting preferred nucleotide substitution model as well as the according value for kappa and the proportion invariant were implemented into the input file for our BEAST runs.

Prior settings for BEAST

Prior settings for the BEAST runs as used for the Bonaire feeding aggregation as well as for each contributory rookery are summarized in *Table 2*. For the Bonaire data set, we additionally performed BEAST simulations with a higher and a lower molecular substitution rate (*Table 2;* as published by Encalada et al. 1996) for the Coalescent BS model to check for the influence of the

intermediate mutation rate we had chosen on population demographic inference and timing of populations declines (if present).

MCMC chain length were chosen so as to allow the chains to converge, the posterior distribution to follow an approximate normal distribution, and estimated sample sizes to exceed 200 (all conditions checked visually analysing the output file in TRACER version 1.5.0 (Rambaut et al. 2014)). This resulted in general chain length of 100,000,000 steps, except for the Aves Island and Costa Rica rookery, for which MCMC chain length was chosen to be 150,000,000 steps instead. Parameters were sampled every 1,000 iterations.

TABLE 2 **Prior settings for BEAST**.

Parameter	setting
Mutation model	*HKY + I + G*
Kappa	34.9475
Frequencies	empirical
Proportion Invariant	0.4120
Molecular clock model	*Strict Clock*
Clock rate, *mean*	$1.8*10^{-8}$ substitution*(site*year)$^{-1}$
Clock rate, *low*	$1.2*10^{-8}$ substitution*(site*year)$^{-1}$
Clock rate, *high*	$2.4*10^{-8}$ substitution*(site*year)$^{-1}$
Priors	*Coalescent Bayesian Skyline* or *Coalescent Constant Population*
Tree	random tree
Distribution	*Jeffreys*
MCMC	
Chain length	100,000,000 iterations
Log every	1,000 iteration

Prior settings for our BEAST runs as specified in BEAUti (implemented in the BEAST2 package, Bouckaert et al. 2014). Parameters for the mutation model had been determined using jModelTest; molecular clock rates are based on values reported in literature for green sea turtles (Encalada et al. 1996). Simulations had been run for both, the Coalescent BS model as well as the Coalescent CP model for each rookery and for the Bonaire feeding aggregation to evaluate which one fitted the observed data best. MCMC chain length had been chosen so as to allow the chains to converge, and estimated sample sizes to reach values larger than 200.

Bayesian Skyline plots, statistical analyses, estimating effective population size, and statistics
Convergence of the MCMC chains was checked and results were analysed using TRACER. We generated Bayesian Skyline plots (Drummond et al. 2005) to visualize the population demographic history as the posterior distribution of theta, θ (the product of effective breeding population size, N_{ef}, and the generation length, τ) (over time in TRACER (choosing the step-wise (constant) Bayesian Skyline variant, 100 bins and no tip dates as settings). Using the Bayesian Skyline plots, we also estimated the time period within which our data were informative regarding demographic changes, since an apparently stable theta in the more distant past of the inferred demographic history indicates that almost no events informing the population

dynamics exist anymore and that theta is due almost exclusively to the priors rather than the data (Bouckaert et al. 2014, Heled 2016).To test the Coalescent BS model against the Coalescent CP model, we calculated Bayes factors (Jeffreys 1935, Kass and Raftery 1995) using 1000 bootstraps replicates in TRACER, and interpreted the results as proposed by (Jeffreys 1998).

RESULTS

Genetic diversity of Bonaire sea turtles

We successfully sequenced the mtDNA control region (824 base pairs) of 39 previously un-sampled sea turtles from the Bonaire feeding aggregation (*Appendix 3*). Combining these samples with previously sequenced data from Bonaire, we based our analyses on 133 sequences of a length of 486 base pairs.

We found 19 polymorphic sites and 12 haplotypes (*Table 3*). CM-A3 and CM-A5 were the most frequent haplotypes.

Haplotype diversity, *h*, was found to be intermediate, if slightly below the average ($\hat{h}$=0.631) of our Caribbean and Atlantic data set, at *h*=0.621. Nucleotide diversity (π=0.0120) was the highest among all Caribbean and Atlantic feeding aggregations and rookeries included in our analyses (see *Table 4*).

TABLE 3 **Haplotype frequencies of the Bonaire sea turtle feeding aggregation**.

Haplotype	*numbers of haplotypes*
CM-A1	2 (0)
CM-A2	1 (0)
CM-A3	40 (0)
Pool "CM-A1.1/.2/.3/.4 or CM-A3.1/.2/.3/.4/.5/.6/.7 or CM-A48.1/.2/.3"	19 (19)
CM-A5	39 (0)
Pool "CM-A5.1/.2/.3/.5 or CM–A6.1"	16 (16)
CM-A6	1 (0)
CM-A8	5 (1)
CM-A16	1 (0)
Pool "CM-A16.1/.2 or CM-A68.1"	1 (1)
CM-A17	2 (0)
CM-A20	1 (0)
CM-A21	2 (1)
CM-A22	1 (0)
CM-A29	2 (1)
CM-A47	1 (0)

Haplotype frequencies of the Bonaire sea turtle feeding aggregation from 133 mtDNA control region sequences. Sites with missing data or alignment gaps were not considered.

If our sequences could not be assigned unambiguously to *one* reference haplotype (neither considering short (486 base pairs) nor long (832 base pairs) mtDNA fragments and reference haplotypes), our sequences were assigned to the "haplotype-pool" named according to the reference haplotypes grouped together.

Numbers of haplotypes are given for the whole Bonaire data set; numbers in brackets specify the haplotype frequencies of the samples sequenced in the present study.

Population genetics of Caribbean and Atlantic rookeries and feeding grounds

We found 33 polymorphic sites and 27 different haplotypes in our wider Caribbean and Atlantic data on sea turtle feeding aggregations and rookeries when sites with missing data or alignment gaps were excluded (38 haplotypes when sites with missing data or alignment gaps were not excluded). Overall haplotype diversity was h=0.650 (h=0.702 when sites with missing data or alignment gaps were not excluded (gap as the fifth state)) and nucleotide diversity was π=0.0107. Number of haplotypes, haplotype diversity and nucleotide diversity for each sea turtle feeding aggregation and rookery separately are presented in *Table 4*.

TABLE 4 Measures of genetic diversity of Caribbean and Atlantic sea turtle feeding aggregations and rookeries.

Feeding aggregation	no. of sequences	no. of haplotypes	no. of polymorphic sites	h	π
Argentina*	93	8	7	0.525	0.0019
Ascension Island	50	6	4	0.260	0.0006
Aves Island	30	2	10	0.186	0.0039
Bahamas*	79	6	11	0.370	0.0064
Barbados*	60	8	16	0.773	0.0103
Brazil, Almofala*	117	12	15	0.701	0.0066
Brazil, Rocas Atoll	53	7	10	0.520	0.0018
Brazil, Ubatuba*	113	10	13	0.446	0.0021
Bonaire*	133	12	19	0.621	0.0120
Cape Verde*	44	5	10	0.588	0.0042
Costa Rica	433	5	28	0.163	0.0036
Florida*	62	6	14	0.485	0.0031
North Carolina*	106	12	18	0.729	0.0053
Suriname	15	3	25	0.257	0.0091

Number of haplotypes, number of polymorphic sites, haplotype diversity (h), and nucleotide diversity (π) for all Caribbean and Atlantic feeding aggregations (marked by a star) and rookeries (unmarked) included in our analyses of mtDNA control region sequences (486 base pair length). Values for the Bonaire feeding aggregation refer to the combined data set of literature (Velez-Zuazo 2008) and newly sequenced data.

Population structure and connectivity among Caribbean and Atlantic rookeries and feeding grounds

F_{ST} values and estimated migration among Caribbean and Atlantic feeding aggregations and rookeries are presented in *Table 5*.

TABLE 5 F_{ST} **values and number of migrants per generation among Caribbean and Atlantic sea turtle feeding aggregations and rookeries**.

	AR*	AS	AV	BAH*	BAR*	BAL*	BRO	BUB*	BON*	CV*	CR	FL*	NC*	SUR
AR*		0.09	0.39	0.71	0.37	0.08	0.11	0.01	0.30	0.11	0.80	0.84	0.75	0.09
AS	4.88		0.59	0.76	0.42	0.15	0.06	0.03	0.35	0.30	0.85	0.88	0.79	0.14
AV	0.80	0.35		0.67	0.37	0.24	0.55	0.46	0.25	0.10	0.77	0.80	0.72	na
BAH*	0.20	0.16	0.25		0.17	0.51	0.71	0.71	0.13	0.65	0.03	0.05	0.05	0.36
BAR*	0.87	0.70	0.84	2.39		0.15	0.36	0.36	0.01	0.31	0.42	0.32	0.21	0.18
BAL*	6.08	2.92	1.58	0.48	2.75		0.12	0.08	0.14	0.07	0.63	0.66	0.55	0.08
BRO	4.09	7.97	0.41	0.20	0.87	3.85		0.05	0.31	0.29	0.81	0.84	0.75	0.15
BUB*	37.96	15.13	0.60	0.21	0.90	6.08	10.61		0.30	0.17	0.80	0.84	0.75	0.11
BON*	1.19	0.95	1.52	3.38	55.06	3.07	1.10	1.19		0.23	0.23	0.24	0.17	0.13
CV*	4.22	1.16	4.31	0.27	1.14	6.75	1.25	2.41	1.72		0.75	0.78	0.69	0.02
CR	0.12	0.09	0.15	16.17	0.70	0.30	0.12	0.12	1.70	0.17		0.02	0.09	0.43
FL*	0.10	0.07	0.12	8.76	1.05	0.26	0.09	0.10	1.55	0.14	20.33		0.04	0.44
NC*	0.17	0.13	0.19	9.50	1.89	0.40	0.17	0.17	2.41	0.22	5.06	12.32		0.39
SUR	5.25	2.97	na	0.89	2.34	5.83	2.81	3.96	3.41	22.23	0.66	0.63	0.78	

FST values (above diagonal) among all Caribbean and Atlantic feeding aggregations (marked with a star) and rookeries (unmarked) included in our analyses, as well as number of migrants per generation (below diagonal) as expected under a simplistic island model. Sites with alignment gaps were considered (gaps as the fifth state). Feeding aggregations and rookeries were abbreviated as follows: AR (Argentina); AS (Ascension Island); AV (Aves Island); BAH (Bahamas); BAR (Barbados); BAL (Brazil, Almofala); BRO (Brazil, Rocas Atoll); BUB (Brazil, Ubatuba); BON (Bonaire); CV (Cape Verde); CR (Costa Rica); FL (Florida); NC (North Carolina); and SUR (Suriname).

Pair-wise Chi-square tests performed on F_{ST} values showed significant differentiation between the Bonaire feeding aggregation and most other Caribbean and Atlantic feeding aggregations and rookeries (all except Aves Island and Suriname; *Table 6*). The feeding aggregations were also significantly differentiated from one another, as well as the main contributory rookeries (except Aves Island and Suriname again; see *Appendix 1* and *2*, respectively).

TABLE 6 Pair-wise Chi square test on F_{ST} values.

Feeding aggregation or rookery compared with Bonaire	Chi square	p-value and significance	df
Argentina*	143.846	0.0000 ***	24
Ascension Island	154.400	0.0000 ***	22
Aves Island	27.328	0.0730 ns	18
Bahamas*	35.948	0.0072 **	18
Barbados*	38.006	0.0088 **	20
Brazil, Almofala*	95.831	0.0000 ***	25
Brazil, Rocas Atoll	164.453	0.0000 ***	24
Brazil, Ubatuba*	175.204	0.0000 ***	25
Cape Verde*	53.624	0.0000 ***	18

Costa Rica	182.810	0.0000 ***	19
Florida*	50.676	0.0001 ***	19
North Carolina*	86.011	0.0000 ***	23
Suriname	27.400	0.0957 ns	19

Results of the pair-wise Chi square test performed on FST values between the Bonaire feeding aggregation and all other Caribbean and Atlantic feeding aggregations (marked with a star) and rookeries (unmarked) considered in this study. Sites with alignment gaps were considered (gaps as the fifth state). Levels of significance are given as: ns, not significant; *, 0.01<p-value<0.05; **, 0.001<p-value<0.01; ***, p<0.001. *df* denotes degrees of freedom.

Demographic history of Bonaire sea turtles

The relatively high amount of genetic diversity within the Bonaire sea turtle feeding aggregation enabled us to extend the timeframe of our Coalescent BS analyses up to 250,000 years under an intermediate molecular substitution rate ($1.8*10^{-8}$ substitutions*(site*year)$^{-1}$; *Figure 2*). However, the apparently constant theta extending from approximately 10,000 years ago towards the more distant past indicates that our data did not contain sufficient genetic variation informing demographic changes past the most recent 10,000 years. Within the recent past, the mean inferred theta showed a possible weak decline starting 5,000 to 6,000 years ago. However, the confidence interval also allowed interpretations of a constant population size, and, within the last 1,000 years approximately, even a strong decline in theta. Bayes factors indicated that the Coalescent BS model fits our combined Bonaire data better than the Coalescent CP model does (3.194 compared to 0.313, respectively).
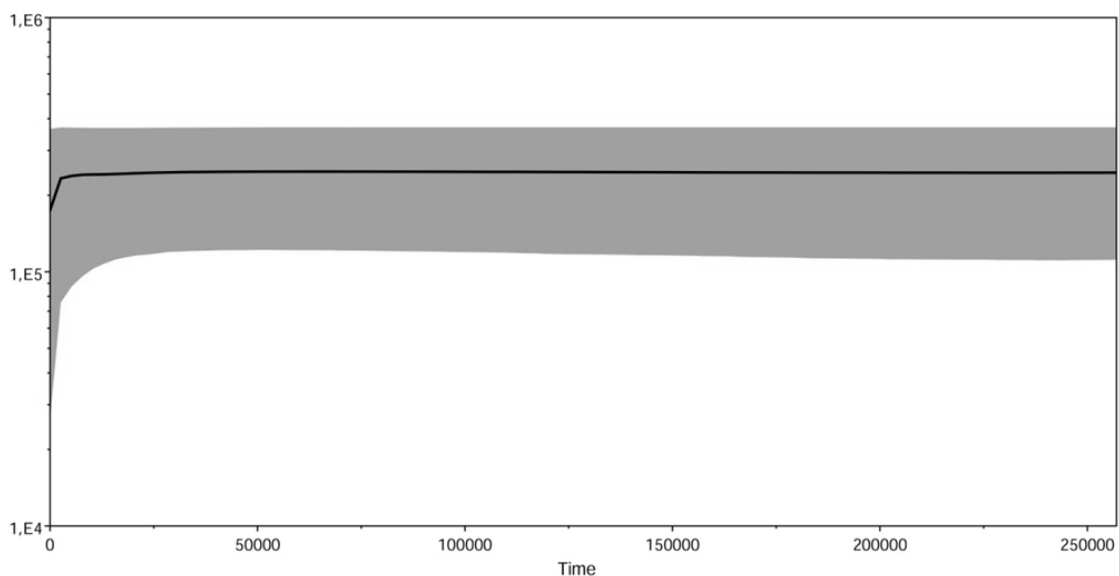
FIGURE 2 Bayesian Skyline plot of the Bonaire feeding aggregation. Inferred theta over time for the green sea turtle mtDNA control region sequences from the Bonaire feeding aggregation under an intermediate molecular substitution rate. The mean inferred theta is shown as black line; the grey area is the confidence interval.

Decreasing the molecular clock rate extended the timeframe of the coalescent BS analyses of the Bonaire feeding aggregation to 350,000 years (*Figure 3*), but our data remained informative only within the most recent 10,000 years. There were slightly stronger indications of a recent population decline at about the same time point as in the estimations assuming an intermediate molecular clock rate (around 4,000 years ago), but estimates of theta were generally a little higher. The confidence interval was narrower than under an intermediate molecular clock rate,

but also widened in the recent past. Bayes factors indicated that the Coalescent BS model fitted the observed data better than the Coalescent CP model (2.531 compared to 0.395, respectively).
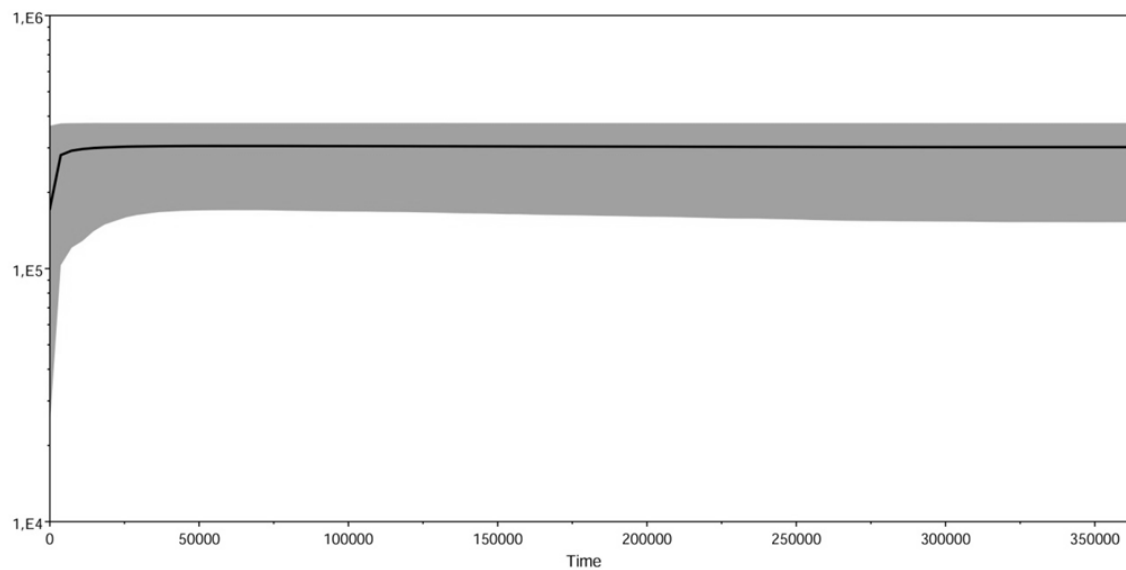
FIGURE 3 Bayesian Skyline plot of the Bonaire feeding aggregation under a low molecular substitution rate. Inferred theta over time for the green sea turtle mtDNA control region sequences from the Bonaire feeding aggregation under a low molecular substitution rate. The mean inferred theta is shown as black line; the grey area is the confidence interval.

Increasing the molecular clock rate to $2.4*10^{-8}$ substitutions*(site*year)$^{-1}$ widened the confidence intervals of the inferred theta in the recent past and restricted the informative time period to the most recent 5,000 years, approximately (*Figure 4*). Bayes factors indicated again that the Coalescent BS model fitted our data slightly better than the coalescent CP model (1.486 compared to 0.673, respectively).
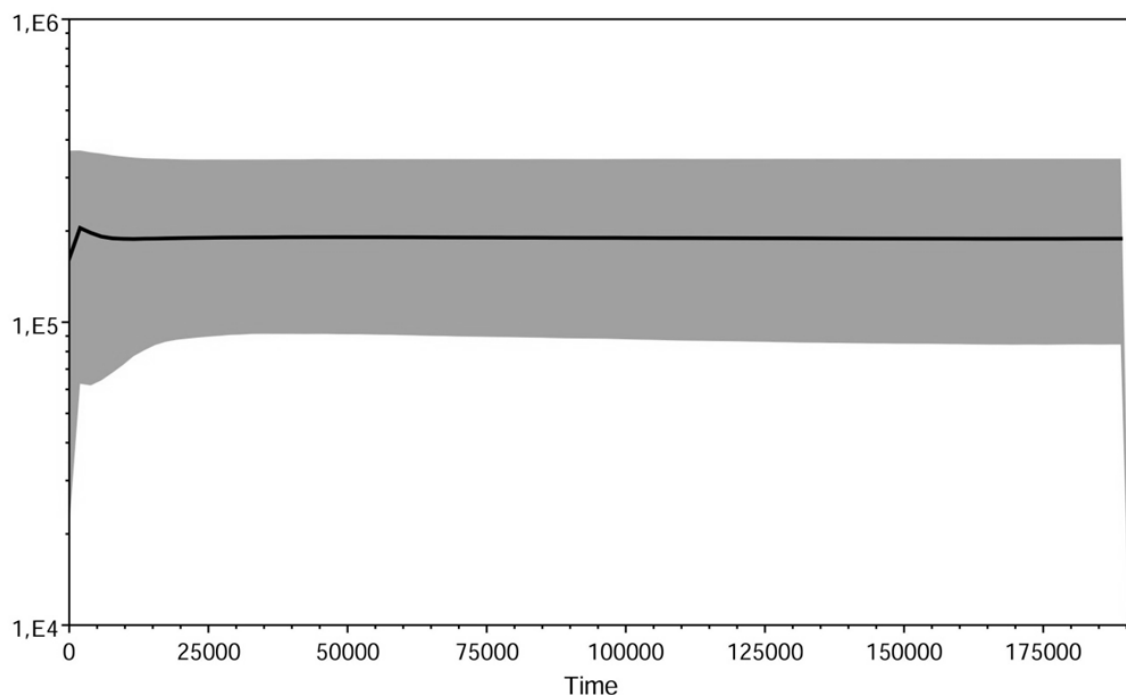
FIGURE 4 Bayesian Skyline plot of the Bonaire feeding aggregation under a high molecular substitution rate. Inferred theta over time for the green sea turtle mtDNA control region sequences from the Bonaire feeding aggregation under a high molecular substitution rate. The mean inferred theta is shown as black line; the grey area is the confidence interval.

Demographic history of main contributory rookeries

The Bayesian skyline plots of the main contributory rookeries differed from each other, but all estimated recent theta around the same values, below a theta of 100,000. However, past thetas differed strongly, with the Costa Rica and Suriname sea turtle rookeries displaying much higher estimated values of historic theta (values similar to the Bonaire estimates) than the other rookeries (*Figures 5-9*).

Ascension Island

We were able to infer theta of the Ascension Island sea turtle rookery up to 2,500 years into the past (*Figure 5*). However, the apparently constant theta indicated that there may be insufficient genetic variation in our data, as the consistency of theta is likely due almost exclusively to the priors of our inference instead of the demographic information in our data.

Bayes factors slightly favoured the coalescent BS model over the coalescent CP model (1.338 compared to 0.747, respectively).
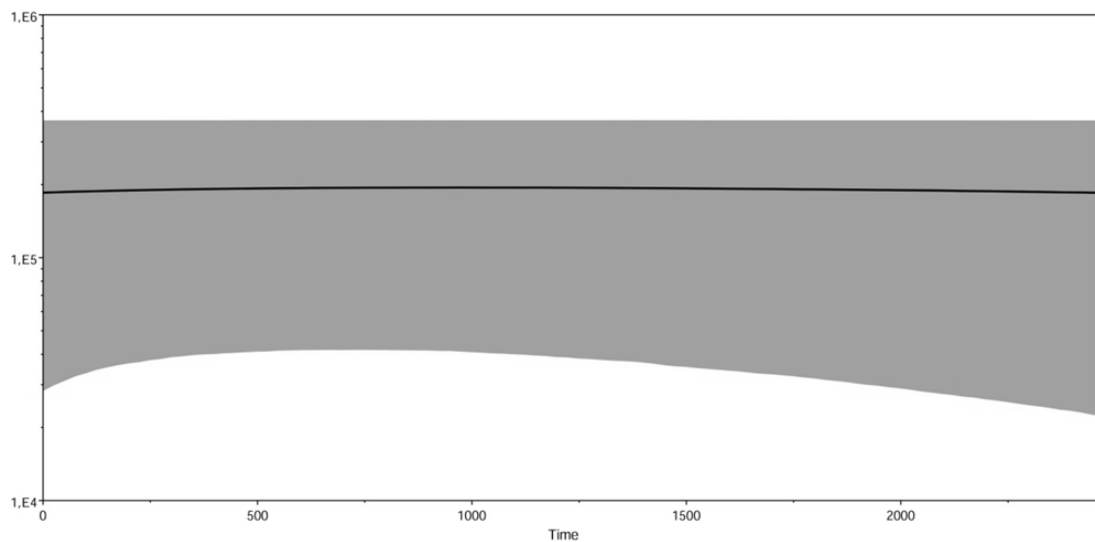
FIGURE 5 **Bayesian Skyline plot of the Ascension Island rookery**. Inferred theta over time for the green sea turtle mtDNA control region sequences from the Ascension Island rookery. The mean inferred theta is shown as black line; the grey area is the confidence interval.

Aves Island

For the Aves Island rookery, the timeframe of our coalescent BS analyses extended to 200,000 years ago (*Figure 6*). However, information regarding demographic changes in our data was likely restricted almost exclusively to the time period between the present and approximately 75,000 years ago. Within the recent past, theta showed signs of a possible strong (more than half an order of magnitude) decline in population size starting around 30,000 years ago. However, the confidence interval widened towards the present and allowed weaker interpretations of the declining signal or even a recent increase in effective population size. Bayes factors strongly supported the coalescent BS model and rejected the coalescent CP model (4.498 compared to 0.222, respectively).
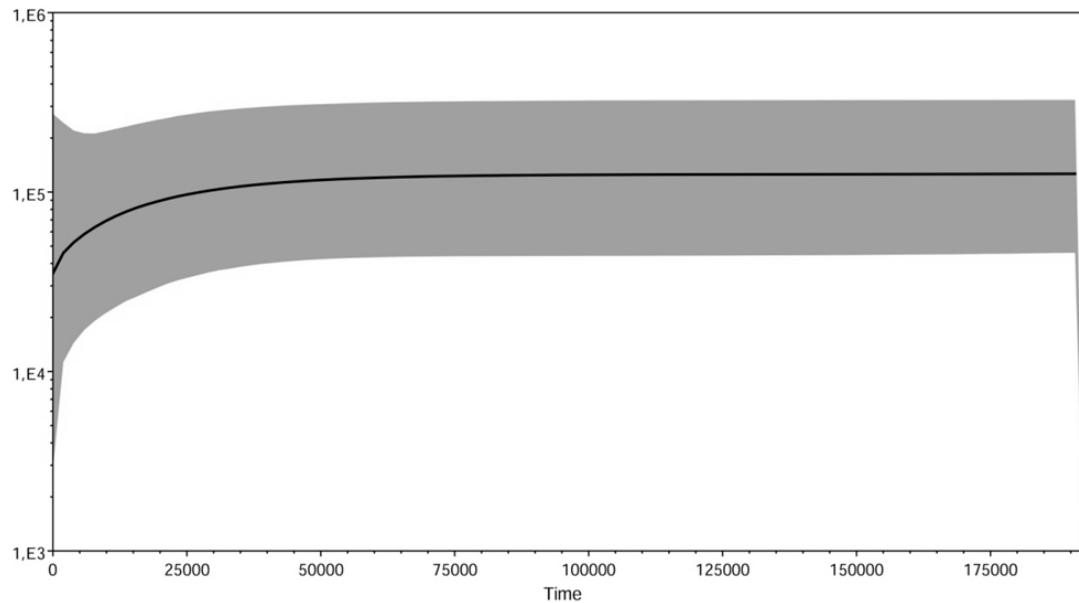
FIGURE 6 Bayesian Skyline plot of the Aves Island rookery. Inferred theta over time for the green sea turtle mtDNA control region sequences from the Aves Island rookery. The mean inferred theta is shown as black line; the grey area is the confidence interval.

Costa Rica

We were able to infer theta of the Costa Rica rookery until 850,000 years ago (*Figure 7*). However, information regarding demographic changes in our data was likely restricted almost exclusively to the time period between the present and approximately 100,000 years ago. Within that time, theta decreased strongly (more than half an order of magnitude) . The Confidence interval also allowed a weaker interpretation of the decrease, but also a decrease of nearly two orders of magnitude. Bayes factors indicated that the coalescent BS model was strongly preferred over the coalescent CP model (624.166 compared to 0.002, respectively).
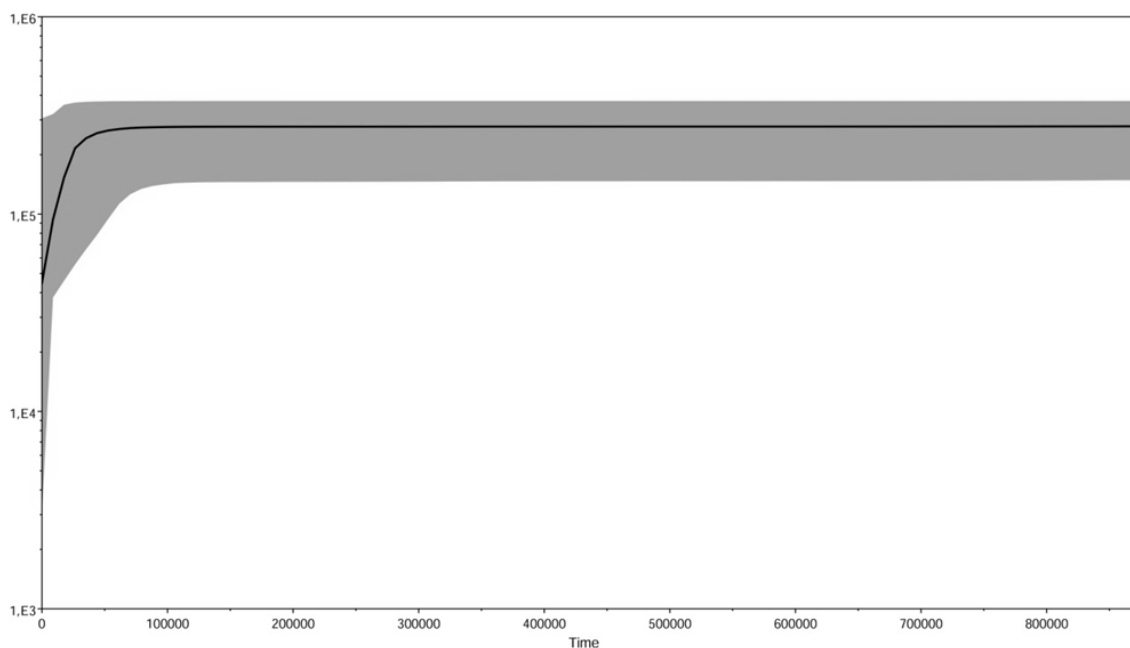
FIGURE 7 Bayesian Skyline plot of the Coast Rica rookery. Inferred theta over time for the green sea turtle mtDNA control region sequences from the Costa Rica rookery. The mean inferred theta is shown as black line; the grey area is the confidence interval.

Rocas Atoll (Brazil)

For the Rocas Atoll sea turtle rookery, coalescent BS analyses could be extended up to 150,000 years ago (*Figure 8*). Theta remained apparently constant and uninformative over that time period. Bayes factors slightly preferred the Coalescent BS model (1.302) over the Coalescent CP model (0.768).
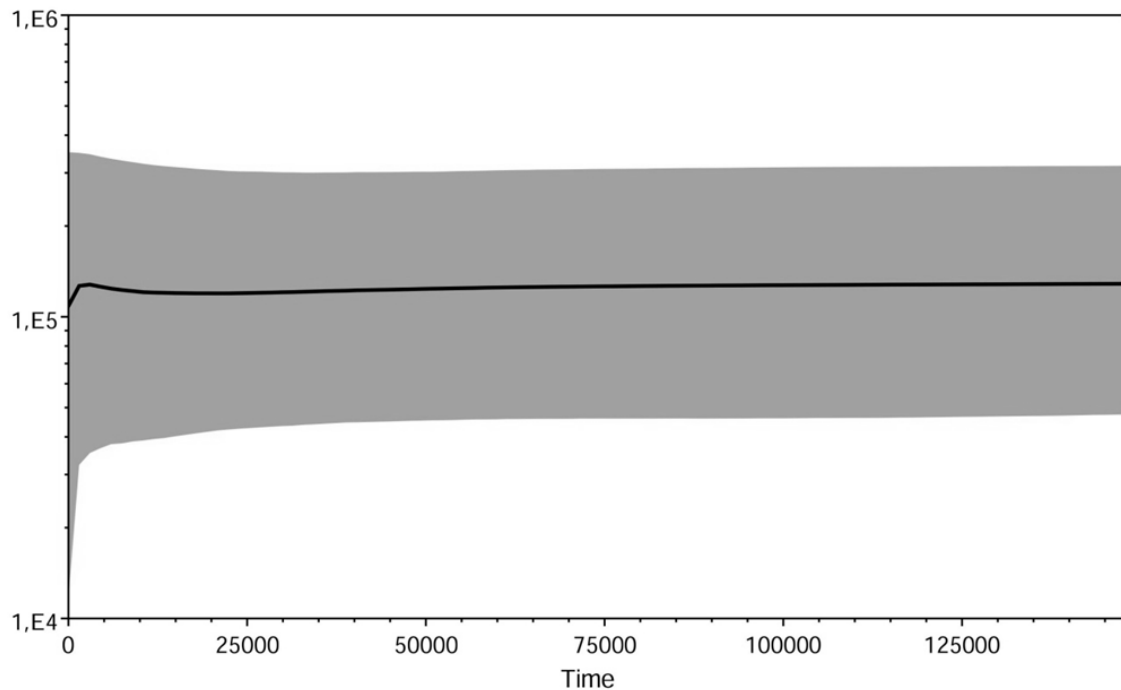
FIGURE 8 Bayesian Skyline plot of the Rocas Atoll rookery. Inferred theta over time for the green sea turtle mtDNA control region sequences from the Rocas Atoll rookery. The mean inferred theta is shown as black line; the grey area is the confidence interval.

Suriname

We were able to extend the coalescent BS analyses for the Suriname sea turtle rookery up to 1,000,000 years ago (*Figure 9*). However, information regarding demographic changes in our data was likely restricted almost exclusively to the time period between the present and approximately 150,000 years ago. Within that time period, the inferred theta described a strong decline. However, the confidence interval widened towards the present and also allowed interpretations of a relatively weak or a very strong decline in theta. Bayes factors clearly favoured the coalescent BS model over the coalescent CP model (13.123 compared to 0.076, respectively).
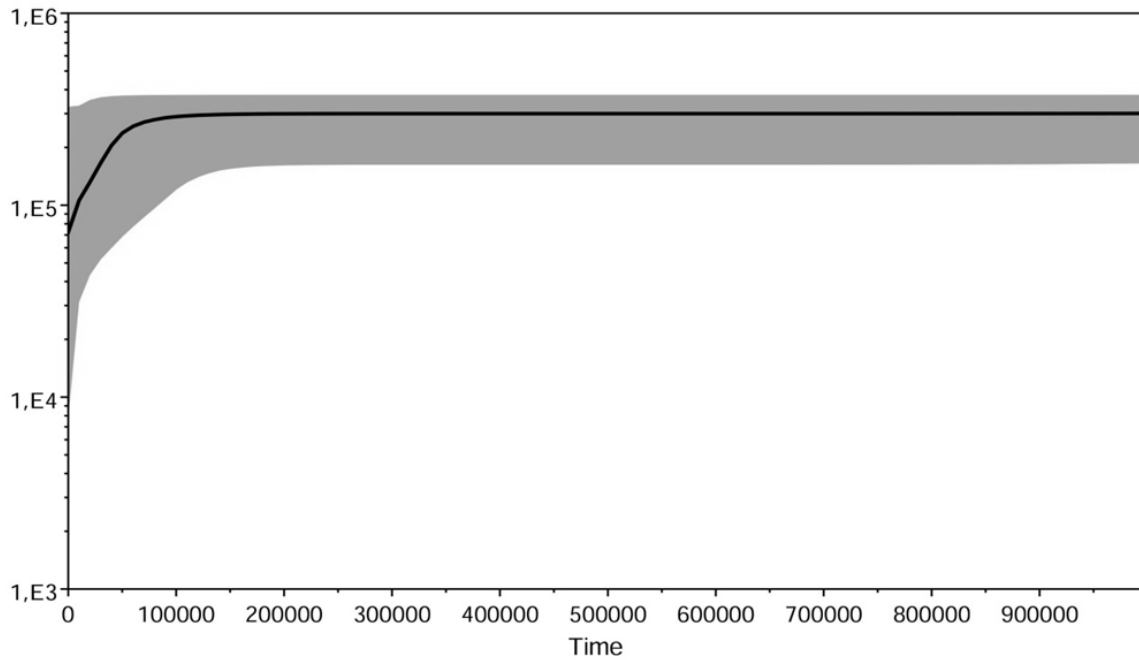
FIGURE 9 Bayesian Skyline plot of the Suriname rookery. Inferred theta over time for the green sea turtle mtDNA control region sequences from the Suriname rookery. The mean inferred theta is shown as black line; the grey area is the confidence interval.

Main contributory rookeries combined
For the combined main contributory rookeries data set, we were able to extend our Bayesian Skyline analyses until 850,000 years into the past (*Figure 10*). However, information regarding demographic changes in our data was likely restricted almost exclusively to the time period between the present and approximately 50,000 years ago. Within that time period, the mean inferred theta indicated a strong decline in population size that continued until present; however, the confidence interval also allowed the interpretation of a near-constant populations size over time.
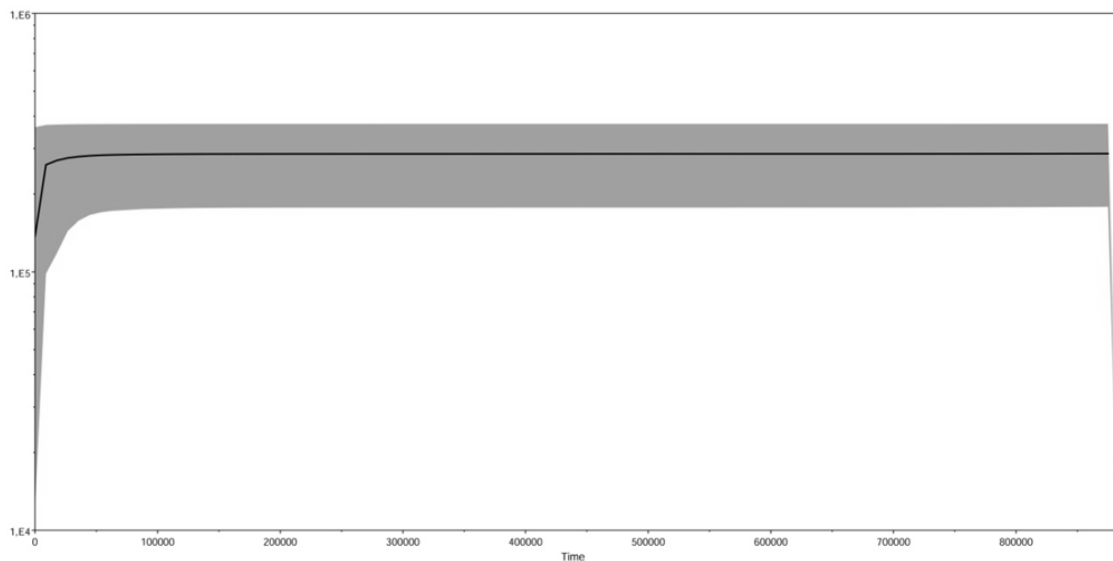
FIGURE 10 Bayesian Skyline plot of the combined contributory rookeries. Inferred theta over time for the combined green sea turtle mtDNA control region sequences from all contributory rookeries. The mean inferred theta is shown as black line; the grey area is the confidence interval.

The structure of this discussion follows the three main aspects of this thesis: 1), the investigation of the Bonaire sea turtle feeding aggregation, discussing the genetic diversity and the connectivity to other Caribbean and Atlantic sea turtle feeding aggregations and rookeries, and inferring the demographic history. 2), the discussion of whether the demographic history inferred for the Bonaire feeding aggregation "mirrors" its main contributory rookeries', or whether it displays local patterns. And 3), the implications of sampling mixed stock aggregations on population demographic inferences, suggesting a strong role of migration and indicating consequential further analyses to strengthen this hypothesis.
We end with our result's implications for the conservation and management of the Bonaire green sea turtle feeding aggregation.

The Bonaire feeding aggregation and its demographic history
Genetic diversity, population structure and connectivity
Green sea turtles around Bonaire showed the highest level of nucleotide diversity reported for any Caribbean or Atlantic green sea turtle feeding aggregation or rookery included in the present study. This high value agrees with the observation that green sea turtle feeding aggregations are composed of individuals originating from different rookeries (e.g., Bass et al. 1998, Bass and Witzell 2000, Bass et al. 2006, Lahanas et al. 1998, Luke et al. 2004, Naro-Maciel et al. 2007, and review by Bowen and Karl 2007), and the assumption that feeding aggregations therefore display generally higher levels of genetic diversity than rookeries do. Haplotype diversity was intermediate compared to the other feeding grounds and rookeries. Compared to literature (Encalada et al. 1996, re-analysed in Reece et al. 2005), nucleotide diversity at Bonaire is high (π=0.012 compared to π=0.010 for 9 Atlantic and Mediterranean populations) and haplotype diversity is low (h=0.621 compared to h=0.830 for the same 9 populations).
We report 12 haplotypes (13 if the full length of the mtDNA fragments sequenced in the current study is considered), of which the two most frequently found haplotypes, CM-A3 and CM-A5, dominate the genetic composition of the western and eastern Caribbean basin, respectively (later also the west Atlantic; Bjorndal et al. 2005).
The Bonaire feeding aggregation was significantly differentiated from most other Caribbean and Atlantic feeding aggregations and rookeries included in this study (all except of Aves Island and Suriname). While we expected Bonaire, as a mixed aggregation, to differ from the rookeries, the structure among the Caribbean and Atlantic feeding aggregations somewhat surprised and indicates that foraging populations are not homogenous across the Caribbean Sea and west Atlantic. Bowen et al. (2007) reports similar heterogeneity for Caribbean feeding aggregations of hawksbill sea turtles. This heterogeneity might be explained by a preference in sea turtles to forage in feeding aggregations closer to their rookery of origin (correlations between recruitment and distance have been reported by e.g., Bass and Witzell 2000, Reece et al. 2005), or possibly by sea turtles from very large rookeries (e.g., Costa Rica) recruiting to only very few feeding aggregations, "imprinting" their genetic signal on those rookeries and making them distinct from the others.
In general, knowledge of the structure among the studied feeding aggregations and the rookeries that potentially are connected through migration is important to consider when deciding on management strategies (e.g., Bowen et al. 1992, Schindler et al. 2010, and see below) as well as when interpreting inferred demographic histories (Heller et al. 2013, and see below).
We estimated genetic diversity, as well as F_{ST} values and number of migrants per generation based upon mtDNA fragments, and therefore, we only considered the genetic diversity,

population structure and connectivity contributions of *female* sea turtles. Simplifying by focusing on females only brings direct advantages - for example that the origin of sea turtles in mixed feeding aggregations can be determined (e.g., Bowen and Karl 2007, Norman et al. 1994) owing to the natal homing of female sea turtles (Bowen 1995), a behaviour that had led to strong population structure among rookeries (reviewed in Bowen and Karl 2007, Reece et al. 2005). However, the loss of information from excluding male gene flow becomes a drawback if male gene flow is substantial (as has been documented for different regions by e.g., Bowen et al. 1992, FitzSimmons et al. 1997, Karl et al. 1992, and Roberts et al. 2004; but see also Carreras et al. 2007 for loggerhead sea turtles). If male gene flow was high among the feeding aggregations and rookeries we studied, the F_{ST} values we estimated would likely have overestimated real values, while our number of migrants per generation would have underestimated real values.

Demographic history and inferred theta of the Bonaire feeding aggregation
We inferred a possible subtle recent decline in genetic diversity for the Bonaire feeding aggregation (*Figures 2* to *4*). However, Bayesian skyline plots are prone to confound the effect of structure with declines in population size as they derive theta from the inferred genealogies (Pannell 2003; based on the work of Wakeley 1999). Genealogies of structured populations consist of two distinct phases: the recent, so-called "scattering" phase that lasts until all samples lineages have coalesced or migrated, and the older, so-called "collecting" phase, in which lineages have to migrate to the same deme before coalescence can occur (Wakeley 1999). These distinct phases will cause an apparent decline in estimates of effective population size going from the ancient (collecting phase) to the recent (scattering phase) part of the genealogy(Pannell 2003, Heller et al. 2013).
We have shown that the Bonaire feeding aggregation is significantly differentiated from all main contributory rookeriesexcept Aves Island and Suriname - and that our samples therefore originate from different, structured sub-populations. Hence, we conservatively conclude that the theta inferred from samples of the Bonaire feeding population has slightly declined or stayed constant over the past 6,000 years.
In the section "future challenges" (below), we will discuss how we could account for population structure when interpreting the demographic histories in our follow-up studies.
An additional uncertainty of population genetic studies lies in the assumptions on the mutation rate μ (e.g., Hoffman et al. 2011, Scally 2016). The mutation rate depends on multiple factors which may have varied substantially over time, and it also depends on the genomic regions of interest and the level of sensitivity and specificity of the analyses (Scally 2016). To compensate for this source of uncertainty, we reconstructed two alternative Bayesian skyline plots for the Bonaire feeding aggregation, one using a higher and one using a lower mutation rate. The Bayesian Skyline Plots under the three different mutation rates recovered approximately the same demographic trends, except that under the lower mutation rate, the inferred theta was slightly higher than under the other two mutation rates. Furthermore, under the higher mutation rate, confidence intervals were slightly wider than under the other two mutation rates.

Is the Bonaire feeding aggregation's demographic history "imported"?
Demographic history and inferred theta of the main contributory rookeries
We inferred possible strong demographic changes for three main contributory rookeries (Aves Island, Costa Rica, and Suriname). None of the studied contributory rookeries showed recent increases in theta. The genetic data of two rookeries, Ascension Island and the Rocas Atoll in Brazil, did not contain enough information on demographic dynamics and hence the inferred theta was shaped mainly by the priors of our analysis, and was therefore uninformative. A

possible reason for such a loss of demographic information could be a strong recent bottleneck, or, in the case of Ascension Island, may lie in the fact that its samples were strongly dominated by one specific haplotype (CM-A8; constituting 86% of all haplotypes; *Table 1*). This may obstruct the reconstruction of the demographic history, since genealogies coalesce very fast. The informative part of the demographic histories of all rookeries but Ascension Island and the Rocas Atoll extend back in time long enough to allow analyses of the genetic diversities before and after the Last Glacial Maximum (15,000 to 30,000 years ago; Miller et al. 2010) that was associated with major environmental disturbances (e.g., Encalada et al. 1996, Naro-Maciel et al. 2014, Reece et al. 2005). Surprisingly, none of the rookeries except Aves Island show declines in theta during or following these events that could be associated with the environmental disturbances. Furthermore, the recent declines in theta started longer than 500 years ago, and thus rule out human exploitation as the primal cause of the declines. This might indicate that the genetic diversity of Caribbean and west Atlantic green sea turtles may not have been eroded strongly by past climatic events or human impact (but see comments below about the reliability of genetic diversity estimates concerning the more recent past), and may serve as "buffer" against at least some future climatic changes (compare Schindler et al. 2010 on the capacity of genetic diversity to "buffer" environmental or ecosystem changes, termed "portfolio effect"). Reece et al. (2005) also found only a minimal net depression effect of past climatic changes on the current effective population size of green sea turtles in the Atlantic and Mediterranean population. However, re-colonization events after (partial) local extinctions could have eliminated population declines from the presently available genetic information (and would require ancient DNA analyses). Similarly, old demographic changes can be "erased" by more recent demographic changes (e.g., Bunnefeld et al. 2015) or immigration (e.g., Cornuet and Luikart 1996, Keller et al. 2001). We therefore cannot rule out a historic decline in theta with certainty based on its absence in the Bayesian Skyline Plots.

Does the Bonaire feeding aggregation simply "mirror" the demographic histories of the main contributory rookeries?

It seems possible that the Bonaire feeding aggregation mirrors the main contributory rookeries in their demographic histories, evident in the similarity of inferred thetas and overlapping confidence intervals of the Bonaire feeding aggregation and the rookeries at Aves Island, Costa Rica, and Suriname, as well as the combined contributory rookeries. We therefore hypothesise that (sea turtle) feeding aggregations that consist of sea turtles from different origins, like Bonaire, are likely to "mirror" the demographic histories "imported" from the rookeries of origin rather than to display *local* past population size changes.

Suggestions on further investigations to test this hypothesis are presented in the section "future challenges" (below).

Implications of sampling mixed (sea turtle) aggregations for population demographic inferences

Methodological implications

Based on the similarity of the demographic history inferred for the Bonaire feeding aggregation with the main contributory rookeries', we hypothesise that mixed aggregations cannot be analysed informatively for their demographic histories without carefully considering migration patterns. Without sufficient knowledge of migration into and from mixed stocks, we cannot be sure to which sub-population(s) the inferred demographic histories actually apply or belong to. Management strategies derived from such demographic histories might therefore better apply to (sea turtle) rookeries at distant locations than to the studied feeding aggregations, or even to an

only theoretically existing population composed of individuals from several contributory rookeries.

Ignoring this fact, demographic history reconstructions of feeding aggregations are preformed rather often, for example in fisheries sciences (J.P. van der Zee, pers. com.), and among other purposes used to calculate catch quota (e.g., for sea turtles: Heppell and Crowder 1996). This is dangerous, as one might dramatically overfish or deplete single, unique contributory areas if the quota for the mixed aggregation is based on inferences that are imprinted with the genetic signal of genetically diverse contributory areas.

Therefore, we suggest that management recommendations based on inferred demographic histories may not only be implemented *locally* (in the mixed aggregation in which the samples had been collected), but in a wider management-unit framework, including both, the mixed aggregation *and* the contributory areas. Furthermore, we recommend that future analyses aiming at developing management strategies or inferring population size changes over time for a mixed (sea turtle) aggregation 1), implement migration information (if not available, generating it using methods such as the mixed stock analyses (Grant et al. 1980, Pella and Milner 1987; applied to sea turtles: e.g., Bass 1999, Bjorndal et al. 2006, LaCasella et al. 2013, Okuyama and Bolker 2005)), 2), discuss their sampling scheme and its impact on the results (Heller et al. 2013, and see comments on population structure below), and 3), evaluate their conclusions' spatial and temporal applicability (see below).

Future challenges
To test our hypothesis that the demographic history inferred for the Bonaire feeding aggregation simply "mirrors" the demographic histories of its main contributory rookeries (an assumption based on the conformity of inferred thetas), we suggest the following further analysis:
First, we propose to perform a mixed stock analysis (preferably including all known Caribbean and Atlantic rookeries) to reveal the most probable origin of the sea turtles in the Bonaire feeding aggregation. Then, the rookeries found to contribute the most sea turtles to the Bonaire feeding aggregation should be sub-sampled randomly, proportionally to their contribution. Combining the sub-samples of the main contributory rookeries, a "theoretical" feeding aggregation data set could be generated. For this data set, the demographic history should be inferred under the same settings as for the real Bonaire feeding aggregation data set, which allows the direct comparison of inferred theta and demographic changes. Should there be no significant difference between the demographic reconstructions of the "theoretical" and the real, observed feeding aggregation after multiple repetitions of sub-sampling and demographic inference (we suggest about 10 times), then our hypothesis that the Bonaire feeding aggregation mirrors the demographic histories of its main contributory rookeries (rather than displaying a distinct, *local* demographic history) would be strongly supported. Should there be a significant difference in demographic reconstructions, then our hypothesis would be falsified. Furthermore, to not only account for migration, but also for population structure when interpreting demographic histories (as proposed by Heller et al. 2013), we suggest to add a simulation study, as could be the following:
First, two sets of several green sea turtle rookeries should be simulated, one without, and one with structure among rookeries (using our reported F_{ST} values). Both data sets should then be sub-sampled to generate artificial feeding aggregations (potentially under sampling schemes mimicking observed patterns, as could be isolation-by-distance (e.g., Bass and Witzell 2000, Reece et al. 2005) or contributions proportional to the rookery's size (Lahanas et al. 1998)). From those artificial feeding aggregations, samples should be drawn repetitively and used to infer the demographic histories of the feeding aggregations. These demographic histories should

then be compared to the ones inferred for the (combined) rookeries of each data set. Based on the difference in inferred theta between the rookeries and their feeding aggregations, and the difference in theta between the not-structured and the structured data set, we could estimate the imprecision of the theta inferred for the Bonaire feeding aggregation (comprising sea turtles from structured rookeries), and whether the inferred decline in theta is more likely due to structure among the contributory rookeries or to an actual decrease in effective population size.

Implications for the management of the Bonaire feeding aggregation

The Bonaire feeding aggregation has been found to be unique in its high nucleotide diversity and significantly differentiated from nearly all other feeding aggregations and rookeries considered in this analysis, which highlights the importance of its conservation. Based on demographic inferences, a slight decline in sea turtle genetic diversity might have happened during the past 6,000 years.

No additional strong bottleneck was apparent within the last 500 years of human exploitation; however, such a signal could have been "overwritten" by trends in the potentially less exploited or more resilient (since bigger or genetically more diverse) contributory rookeries, or a shift in the amount of sea turtles contributed by each rookery. Furthermore, sea turtle life history is characterized by longevity, late maturation and low mtDNA mutation rate (compared to estimates for many other vertebrates; e.g., Avise et al. 1992, Bowen et al. 1992, Bowen et al. 1993), warranting decades for trends in effective population size to become detectable (Bowen and Karl 2007).

Additionally, Bayesian skyline plots are not ideally suited to analyse recent population trends (within approximately the last seven generations; P.J. Palsbøll, pers. com.), and analyses addressing such recent changes in effective population size are desirable to complement our results.

All in all, the re-assumption of sea turtle harvesting in Bonaire waters might lead to declines in sea turtle abundances far away and possibly beyond reach of impact assessments given the interconnectivity of the Bonaire feeding aggregation with rookeries throughout the Caribbean and Atlantic. This suggests a conservative approach and a need of more studies of current as well as past genetic diversity (that include migration and population structure) before changing current management strategies and before we will be able to estimate the sea turtles' future ability to adapt to global warming and anthropogenic pressure.

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TABLE 7 Pair-wise Chi square test results on F_{ST} values between Caribbean and Atlantic feeding aggregations.

	AR	BAH	BAR	BAL	BUB	BON	CV	FL	NC
AR		141.196 ***	66.186 ***	25.073 *	14.757 ns	143.846 ***	24.341 **	144.130 ***	157.794 ***
BAH			41.874 ***	100.199 ***	155.830 ***	35.948 **	77.220 ***	21.615 **	56.308 ***
BAR				35.401 **	73.474 ***	38.006 **	27.452 ***	36.105 ***	40.964 ***
BAL					34.978 **	95.831 ***	19.769 ns	110.986 ***	127.644 ***
BUB						175.204 ***	38.947 ***	155.846 ***	170.747 ***
BON							53.624 ***	50.676 ***	86.011 ***
CV								83.396 ***	92.361 ***
FL									18.643 ns
NC									

Results of the pair-wise Chi square test performed on FST values between Caribbean and Atlantic feeding aggregations. Sites with alignment gaps were considered (gaps as the fifth state). Level of significance are given as: ns, not significant; *, 0.01<p-value<0.05; **, 0.001<p-value<0.01; ***, p<0.001. *df* denotes degrees of freedom. Abbreviations stand for: AR (Argentina); BAH (Bahamas); BAR (Barbados); BAL (Brazil, Almofala); BUB (Brazil, Ubatuba); BON (Bonaire); CV (Cape Verde); FL (Florida); and NC (North Carolina).

TABLE 8 **Pair-wise Chi square test results on FST values between the main contributory rookeries of the Bonaire feeding aggregation**.

	AS	AV	BRO	CR	SUR
AS		80.000 ***	483.000 ***	24.554 *	60.775 ***
AV			172.200 ***	83.000 ***	5.513 ns
BRO				486.000 ***	162.335 ***
CR					68.000 ***
SUR					

Results of the pair-wise Chi square test performed on FST values between the main contributory rookeries of the Bonaire feeding aggregation. Sites with alignment gaps were considered (gaps as the fifth state). Level of significance are given as: ns, not significant; *, $0.01 < \text{p-value} < 0.05$; **, $0.001 < \text{p-value} < 0.01$; ***, $p < 0.001$. *df* denotes degrees of freedom. Abbreviations stand for: AS (Ascension Island); AV (Aves Island); BRO (Brazil, Rocas Atoll); CR (Costa Rica); and SUR (Suriname).

Table 9 The mtDNA control region sequences of 39 previously un-sequenced green sea turtles of the Bonaire feeding aggregation.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
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CM 29	-	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CM 31	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 32	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 33	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CM 35	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 36	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CM 38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CM 39	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
CM 01	T	C	C	T	T	T	G	-	A	C	A	C	A	G	G	A	A	T	A	A	A	A	G	T	G	T	C	C	A	C	A	C	A	A	A	C	T	A	A	C	T	A	C	C	T	A	A	A	T	T	C	T	C	T	G	C	C	G	T	G
CM 02	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 03	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 04	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 05	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 06	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 07	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 08	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 09	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 10	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 11	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 12	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 13	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 14	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 15	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 16	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 17	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 18	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 19	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 20	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 21	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 22	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 23	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 24	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 25	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 26	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 27	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 28	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 29	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CM 31	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 32	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 33	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 34	-	-	-	-	-	-	-	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	-	-	-	-	-
CM 35	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 36	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CM 38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.	.	.	.	.	.	.	.	.	.	.	.
CM 39	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Alignment of DNA sequences (nucleotide positions 121–180). A dot (.) indicates identity with the reference sequence (CM 01); a dash (-) indicates a gap.

```
Position:  121                                                                                              180
CM 01  C C C A A C A G A A C A A T A C C C G C A A T A C C T A T C T A T G T A T T A T C G T G C A T C T A C T T - A T T T A C
CM 02  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 03  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 04  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 05  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . T . . . . .
CM 06  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 07  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 08  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 09  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 10  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . . . .
CM 11  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . T . . . . .
CM 12  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . A . . . . . . . . . - . . . . .
CM 13  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 14  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 15  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . T . . . . .
CM 16  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . . . .
CM 17  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . T . . . . .
CM 18  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . A . . . . . . . . . - . . . . .
CM 19  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . T . . . . .
CM 20  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 21  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . T . . . . .
CM 22  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 23  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . T . . . . .
CM 24  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 25  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . T . . . . .
CM 26  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . A . . . . . . . . . - . . . . .
CM 27  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . T . . . . .
CM 28  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . A . . . . . . . . . - . . . . .
CM 29  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . T . . . . .
CM 30  - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - . . A . . . . . . . . . - . . . . .
CM 31  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 32  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . T . . . . .
CM 33  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . - . . . . .
CM 34  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . T . . A . . . . . . . . . . . . T . . . .
CM 35  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . . . .
CM 36  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . C . T . . . . .
CM 37  - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - . . . . . . . . . . . . . . . T . . . .
CM 38  . . . . . . . . . . . . . C . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . - . . . . .
CM 39  . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . A . . . . . . . . . - . . . . .
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	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240
CM 01	C	A	A	T	A	G	C	A	T	A	T	G	A	C	C	A	G	T	A	A	T	A	T	T	A	A	C	A	G	T	T	G	A	T	T	T	G	G	C	C	C	T	A	A	A	C	A	T	A	A	A	A	A	A	T	C	A	T	T	G
CM 02	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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CM 33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 34	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 35	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 36	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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CM 38	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CM 39	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

	241	242	243	244	245	246	247	248	249	250	251	252	253	254	255	256	257	258	259	260	261	262	263	264	265	266	267	268	269	270	271	272	273	274	275	276	277	278	279	280	281	282	283	284	285	286	287	288	289	290	291	292	293	294	295	296	297	298	299	300
CM 01	A	A	T	T	T	A	C	A	T	A	A	A	-	T	A	T	T	T	T	A	A	C	A	A	C	A	T	G	A	A	T	A	T	T	A	A	G	C	A	G	A	G	G	A	T	T	A	A	A	A	G	T	G	A	A	A	T	G	A	C
CM 02	.	.	.	.	.	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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CM 04	.	.	.	.	.	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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CM 01	T	T	C	C	T	A	A	A	T	-	A	G	C	T	A	T	T	C	A	C	G	A	G	A	A	A	T	A	A	G	C	A	A	C	C	C	T	T	G	T	T	A	G	T	A	A	G	A	T	A	C	A	A	C	A	T	T	A	C	C
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CM 01	A	G	T	T	T	C	A	A	G	C	C	C	A	T	T	C	A	A	T	C	T	G	T	G	G	C	G	T	A	C	A	T	A	A	T	T	T	G	A	T	C	T	A	T	T	C	T	G	G	C	C	T	C	T	G	G	T	T	A	G
CM 02	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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CM 01	T	T	T	T	T	C	A	G	G	C	A	C	A	T	A	C	A	A	G	T	A	G	C	A	A	C	G	T	T	C	A	T	T	C	G	T	T	C	C	C	C	T	T	T	A	A	A	A	G	G	C	C	T	T	T	G	G	T	T	G
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CM 01	A	A	T	G	A	G	T	T	C	T	A	T	A	C	A	T	T	G	A	A	T	T	T	A	T	-	A	A	C	C	T	G	G	C	A	T	A	C	G	G	T	A	G	T	T	T	T	A	C	T	T	G	C	A	T	A	T	A	G	T
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Alignment positions 601–660:

Taxon	601	602	603	604	605	606	607	608	609	610	611	612	613	614	615	616	617	618	619	620	621	622	623	624	625	626	627	628	629	630	631	632	633	634	635	636	637	638	639	640	641	642	643	644	645	646	647	648	649	650	651	652	653	654	655	656	657	658	659	660
CM 01	A	G	T	T	T	T	T	T	T	T	C	T	C	-	-	T	C	T	G	T	G	T	T	C	T	C	A	G	G	C	C	C	A	C	A	T	A	A	C	T	G	A	T	A	C	C	T	G	C	C	G	A	T	T	C	A	G	T	G	A
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CM 01	A	A	C	T	G	G	A	C	T	T	A	C	G	T	T	T	A	A	A	T	A	T	G	A	T	T	G	G	T	C	G	T	G	C	A	A	A	C	T	G	A	T	T	A	A	T	G	G	T	A	T	T	A	T	T	A	A	G	T	T
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	721	722	723	724	725	726	727	728	729	730	731	732	733	734	735	736	737	738	739	740	741	742	743	744	745	746	747	748	749	750	751	752	753	754	755	756	757	758	759	760	761	762	763	764	765	766	767	768	769	770	771	772	773	774	775	776	777	778	779	780
CM 01	A	A	T	G	C	T	T	A	T	A	A	G	A	C	A	T	A	G	A	A	T	T	T	C	A	C	A	A	T	T	A	A	A	C	C	T	A	A	A	C	A	A	T	G	A	T	C	T	A	C	A	A	C	C	T	A	A	C	T	C
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CM 01	A	T	T	A	T	T	A	A	C	T	G	T	A	C	T	T	T	T	T	A	G	C	T	A	A	A	C	C	C	C	C	C	T	A	C	C	C	C	C	-	-	-	-	-
CM 02	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	-	-	-	-	-
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The aligned mtDNA control region sequences (total length 824 base pairs) of the 39 previously un-sequenced green sea turtle from the Bonaire feeding aggregation. The rows show the consensus sequences of one individual green sea turtle each (coded as CM *X*); the top row of each page indicates the position of the single base pairs. A dot indicates consistency with the reference sequence; a dash indicates missing data or an alignment gab. At polymorphic sites, the divergent base pair is indicated.