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1   **Sand temperatures for nesting sea turtles in the Caribbean: implications for hatchling sex**

2   **ratios in the face of climate change**

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8   **Highlights**

9   • Mean sand temperatures at nest depths were 31.0 °C, ranging from 29.1 °C to 33.3 °C

10   • Rainfall and spring tides had important cooling effects on incubation temperatures

11   • Sex ratios of 3 species of sea turtle were female-biased during the past century

12   • Rising air temperatures will exacerbate the female skew in future populations

13   • Management strategies will be necessary to prevent localised extinction

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16   ABSTRACT

17   A 200-y time series of incubation temperatures and primary sex ratios for green (*Chelonia*

18   *mydas*), hawksbill (*Eretmochelys imbricata*) and leatherback (*Dermochelys coriacea*) sea

19   turtles nesting in St Eustatius (North East Caribbean) was created by combining sand

20   temperature measurements with historical and current environmental data and climate

21   projections. Rainfall and spring tides were important because they cooled the sand and

22   lowered incubation temperatures. Mean annual sand temperatures are currently 31.0 °C (SD

23   = 1.6) at the nesting beach but show seasonality, with lower temperatures (29.1-29.6 °C)

24   during January-March and warmer temperatures (31.9-33.3 °C) in June-August. Results

25   suggest that all three species have had female-biased hatchling production for the past

26   decades with less than 15.5%, 36.0%, and 23.7% males produced every year for greens,

27   hawksbills and leatherbacks respectively since the late nineteenth century. Global warming

28   will exacerbate this female-skew. For example, projections indicate that only 2.4% of green

29   turtle hatchlings will be males by 2030, 1.0% by 2060, and 0.4% by 2090. On the other hand,

30   future changes to nesting phenology have the potential to mitigate the extent of

31   feminisation. In the absence of such phenological changes, management strategies to

32   artificially lower incubation temperatures by shading nests or relocating nest clutches to

33   deeper depths may be the only way to prevent the localised extinction of these turtle

34   populations.

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36   *Keywords*: temperature-dependant sex determination, IPCC, conservation, reptile, lethal

37   temperatures, endangered species

38

1. Introduction

It is widely reported that climate change is having a profound impact on the functioning of ecosystems (Hoegh-Guldberg and Bruno, 2010). Species abundances and distributions are shifting due to the changing environment (Jones and Cheung, 2015; Poloczanska et al., 2013). The breeding phenology of migratory species is also changing in response to environmental change (e.g. McCarty, 2001; Parmesan et al., 1999; Walther, 2010). Furthermore, climate change-induced habitat loss puts species at risk of extinction when no alternative adequate habitat is available (Foden et al., 2013). The risk of climate change is particularly pronounced for marine ectotherms as they conform more closely to thermal tolerance limits than terrestrial ecotherms (Sunday et al., 2012) and, in particular, species whose biology and phenology are intimately linked to temperature (Somero, 2010). Of particular concern are species that exhibit-temperature-dependent sex determination. This applies to the majority of reptiles, including sea turtles. The concern of climate change is of particular importance to sea turtles considering that six out of the seven species are classified as critically endangered, endangered or vulnerable by the International Union for the Conservation of Nature (IUCN, 2014).

One of the conservation challenges for sea turtle ecologists is that climate change is impacting sea turtles in more than just one way. For instance, sea level rise may cause a loss of the beaches on which the females rely to nest (Fish et al., 2008; Fuentes et al., 2009a). Climate change models also predict an increase of rainfall and storm events at certain sites, which may be detrimental to nests as exposure to high levels of water negatively impacts the success of a nest (Patino-Martinez et al., 2014). Increasing air temperatures is also a concern for species that exhibit temperature-dependent sex determination and may lead to skewed sex ratios and local extinctions (Janzen, 1994). As such, increasing temperature was recently identified as one of the biggest threats to sea turtle populations' viabilities (Fuentes and Cinner, 2010).

65   Quantifying how warming temperatures will impact sea turtle populations across

66   the globe is a conservation priority. A recent thread of research concerns the reconstruction

67   of past sex ratios at important breeding sites based on historical air temperature data (e.g.

68   Hays et al., 1999, 2003). These studies are important in informing how primary sex ratios

69   fluctuated in the past. By using climate projections provided by the Intergovernmental Panel

70   on Climate Change (IPCC) it is also possible to make projections on how the primary sex

71   ratios may change in the future. This is of particular interest when trying to assess if a

72   population is at risk of extinction in the near future due to climate change.

73   Current models used to estimate primary sex ratios are primarily based on air

74   temperatures records alone (e.g. Hawkes et al., 2007; Hays et al., 1999, 2003). Such models

75   are proven to be robust but having more variables may improve the model and make the

76   reconstructions more accurate (Fuentes et al., 2009b). Working with the best available

77   model is important when trying to accurately assess how global warming will affect the

78   viability of sea turtle populations across the globe. The current study examines an array of

79   environmental variables that may influence sand temperature of Zeelandia beach, St

80   Eustatius. Two hundred year time-series of incubation temperatures and primary sex ratios

81   for the three species of turtles nesting at this site were then constructed. The results of this

82   study inform on the extinction risks of these populations of sea turtles and help establish

83   whether conservation efforts, such as shading or relocating nests, would be beneficial at this

84   site.

85

2. Methods

2.1. Study site

The island of St Eustatius (17.5°N, 63.0°W) is located in the Lesser Antilles in the North-eastern Caribbean (Figure 1), with a land area of 21 km². Green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*) and leatherback (*Dermochelys coriacea*) turtles nest on St Eustatius. The present study was conducted on Zeelandia beach (encompassing Turtle Beach to the South), a 1.6 km beach on the eastern, windward, exposed coastline of St Eustatius where a monitoring programme of nesting turtles has been underway since 2002 (Debrot et al., 2005; Esteban et al., 2015).

2.2. Environmental variables

Historical rainfall data were obtained from the FD Roosevelt Airport on St Eustatius (distance of 1.4 km from Zeelandia beach) from Weather Underground (www.wunderground.com/history/airport/TNCE, last accessed on 12 August 2014). Daily precipitations were used to calculate monthly means.

Daily tide predictions for St Barthélemy (distance of 43.4 km from St Eustatius) were obtained from the National Ocean and Atmospheric Association (NOAA) (http://tidesandcurrents.noaa.gov, last accessed on 12 August 2014).

Air temperature and sea surface temperature data for the area between 16-18°N and 62-64°W were obtained from the International Comprehensive Ocean-Atmosphere Data (ICOADS) through the National Centre for Atmospheric Research (NCAR) (http://rda.ucar.edu/datasets/ds540.1/, last accessed on 22 May 2015). Data were downloaded at 2-degree spatial resolution from the Enhanced ICOADS Monthly Summary Release 2.5 and filtered to restrict the dataset to months with at least 20 observations. Data were not interpolated to fill in some gaps existing in the data set.

2.3. Air temperature projections

112   Air temperature projections were obtained from the United Nations Development

113   Programme (UNDP). The projected values stem from an analysis of 15 climate models used

114   by the IPCC for the fourth assessment report published in 2007

115   (www.geog.ox.ac.uk/research/climate/projects/undp-cp/, last accessed on 29 May 2015).

116   The Special Report on Emissions Scenarios (SRES) scenario A2 was used for analysis.

117   Projections that were published for the nation of St Kitts and Nevis, two volcanic islands 12.4

118   km to the south–east of St Eustatius, were used. The mean of the IPCC model output was

119   bias-corrected using a "delta" approach: air temperature anomalies relative to the 1970-

120   1999 mean air temperature in St Kitts and Nevis were added to the 1970-1999 mean air

121   temperature observed in St Eustatius. To correct for variability, random variability was

122   added based on the standard deviation of the historical ICOADS air temperature records to

123   the model's output. 1000 runs were generated to capture the overall trend. The UNDP data

124   is available in the form of yearly means and quarterly means. Quarterlies that encompass

125   each turtle species' nesting season as recorded 2002-2012 (JB, NE, STENAPA unpublished

126   data) were used. For the hawksbills the yearly mean was used since this species nests from

127   April until February. For the greens the quarterlies that span from March to November were

128   used since the typical nesting season is from April until October. For the leatherbacks

129   quarterlies that span from March through to August were used as nesting season is from

130   February until July. These specific quarterlies were used during analysis both for the

131   temperature reconstructions and temperature projections.

132

133   **2.4. Sand temperature**

134   Tinytag Plus 2 loggers (Tinytag Plus 2 models TGP-4017 and TGP-4500, Gemini Data

135   Loggers, UK) were used to record sand temperature representative of nests for greens,

136   hawksbills and leatherbacks nesting on Zeelandia beach during the 2011 and 2012 nesting

137   seasons. Temperature measurements were recorded every hour. The loggers were originally

138   calibrated to United Kingdom Accreditation Service (UKAS) standards and are accurate to

139   <0.5 °C (www.tinytag.info, www.geog.ox.ac.uk/research/climate/projects/undp-cp, last

140   accessed on 22 May 2015). To minimize impact on natural conditions during burial of

141   loggers, care was taken to excavate a sand core and then replace it back on top of the

142   logger. This was achieved by hammering a PVC pipe to the desired depth of the logger,

143   creating a vacuum and then removing the pipe full of sand. The depth of the hole was

144   verified using a semi-rigid tape measure, then the logger dropped into the hole and sand

145   emptied out of the pipe on top of the logger. A string was connected to the logger to

146   facilitate relocation of loggers.

147   During the 2011 nesting season, eight permanent loggers were buried at locations

148   along the beach, selected based on historical nesting activities: four at 44.6 cm depth

149   (midpoint between 48.8 cm and 40.4 cm, the mean nest depths for greens and hawksbills

150   respectively) and four at 63.3 cm (mean nest depth for leatherbacks). Mean depths were

151   calculated from records as the midpoint between the top and bottom of clutches of eggs

152   excavated between 2005-2010 (JB, NE, STENAPA, unpublished data).

153   During the 2012 nesting season, eight permanent loggers were buried at locations

154   along the beach: four at 48.8 cm depth, mean nest depth for greens, and four at 63.3 cm,

155   mean nest depth for leatherbacks (JB, NE, STENAPA unpublished data). Four additional

156   loggers were deployed at 63.3 cm depth during March-June 2012. Two additional 'roving'

157   loggers were re-positioned every seven days to record temperature conditions at the range

158   of nest depths from 10 cm depth to 100 cm depth by 10 cm increments. Four complete

159   cycles of 10 cm to 100 cm depth temperatures were recorded during the sample period.

160   All roving loggers were buried on 17/02/2012 and excavated on 01/03/2013 to

161   capture the first nesting activity and incubation period after the final nesting activity

162   (Leatherback 24/04-17/06/2012; Green 29/05-14/11/2012; Hawksbill 17/02-26/12/2012).

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2.5. Sand albedo

Albedo was measured to assess the relative reflection of the sand on Zeelandia beach and its relationship with sand temperature. Albedo measurements were taken with a standard photographic light meter (Sekonic L-778) following methods described in Hays et al. (2001) at the 12 permanent logger locations on Zeelandia beach. Albedo was calculated as the percentage of reflecting incident solar radiation from a surface:

$$\rho_{350\text{-}800} = (L_s/L_G) \times 18\%$$

where L_s is solar reflection of visible light from the sand, L_G is solar reflection of visible light from a grey card (of known albedo 18%) and $\rho_{350\text{-}800}$ is albedo (of the visible light). Albedo values were expressed as percentage (absorptance = 100% – albedo).

2.6. Primary sex ratios

The relationship between incubation temperature and primary sex ratios described in 2014 was used to calculate sex ratios (Laloë *et al.* 2014). A pivotal temperature of 29 °C was used as this temperature is illustrative for all species of sea turtles (Ackerman, 1997).

2.7. Hatchling emergence success

Year-round morning surveys (0600-0800 h local time) of Zeelandia beach have taken place since 2002 according to a standard protocol for nesting beaches (Eckert *et al.,* 1999). Any indication of turtle activity (i.e. tracks, sand disturbed in a way that was characteristic of nesting) was documented and the presence of eggs confirmed through careful digging by hand. Nightly beach patrols were conducted during peak nesting seasons from April-October (resources permitting).

Hatching success of recorded nests at Zeelandia beach was estimated from 2005-2010. Close to the expected hatching dates (after 50 days of incubation) the nest triangulation data were used to mark the site of the egg chamber. This area was closely

190   monitored for evidence of hatching: a depression in the sand, hatchling tracks or hatchlings.

191   When any signs of hatching were observed the nest was excavated after 48 hours; if no signs

192   of hatching were recorded the nest was excavated after at least 70 days from the date the

193   eggs were laid. During an excavation, the nest contents were carefully removed from the

194   egg chamber and inventoried. The data recorded for each excavated nest included the

195   numbers of: empty shells (representing the number of hatched eggs), hatchlings, unhatched

196   eggs (categorised as No Embryo, Embryo, Full Embryo), pipped eggs, predated eggs,

197   deformed embryos, yolkless eggs; and depth of the top and the bottom of the egg chamber).

198

199   **3.   Results**

200   3.1. **Sand temperature and environmental variables**

201   Five loggers were lost due to beach erosion or hurricanes. Loggers lost mid-season were

202   replaced with new loggers. Data from the 15 loggers that were successfully retrieved were

203   downloaded using Tinytag Explorer 4.7 and checked to ensure that logger time was

204   synchronised with local time at the field site (GMT-4 h). Datasets were reviewed and data

205   before logger deployment and after logger retrieval were removed. When processing the

206   data monthly means were used. We excluded months for which days of data were missing

207   from the analysis. Statistical analyses were performed using R (R Core Team, 2015).

208   Monitoring of sand temperature at mean green, hawksbill and leatherback turtle

209   nest depths on Zeelandia beach during 2011-2013 provided 17 complete months of data

210   from 15 permanent logger stations and a further 12 months of data from two roving loggers.

211   Sand temperature tended to show seasonal variation, increasing during spring and summer

212   towards a maximum in the months of July, August and September (Figure 2) which coincided

213   with peak nesting months of greens and hawksbills.

214   Rainfall and spring tides could be associated with temperature drops, either

215   together or independently. Despite influencing sand temperatures, rainfall and spring tides

216   were not good predictor variables for sand temperature.

217

218   3.2. **Importance of depth**

219   The results from the roving temperature loggers (depth range: 10–100 cm) helped

220   understand the effect of depth on sand temperature at previously-recorded maximum nest

221   depths for the study site. Sand temperatures at shallower depths were consistently higher

222   than at deeper depths; the temperature range was highest during hotter months. Results for

223   the roving temperature loggers at depths below mean nest depths showed a general pattern

224   of warmer near-surface sand temperatures and cooler temperatures at the maximum

225   recorded nesting depth of 100 cm. For example, in April 2012 on Zeelandia beach, the

226   temperature at 40-60 cm (the depth of the permanent loggers) averaged 30.5 °C while the

227   mean temperature at 100 cm was 1.0 °C cooler. This general pattern occurred in different

228   months although temperature did not always continue to decrease below 80 cm depth,

229   perhaps due to the short term cooling effect of rainfall and spring tide on mean

230   temperatures during some weeks (Figure 3).

231

232   **3.3. Sand albedo**

233   On Zeelandia beach albedo $\rho_{350-800}$ was measured at the 12 permanent logger

234   stations on 10 separate days between March-June 2012. The beach did not appear uniform

235   in coloration: lighter areas appear in front of sandstone cliffs and darker areas near the

236   rainwater gulleys. This impression was not supported by albedo measurements which

237   revealed minor intra-beach variation ranging from 80.8% to 86.1% (mean $\rho_{350-800}$ values;

238   mean SD = 2.7%). The relationship between sand temperature at nest depths and the

239   absorption of incident solar radiation by the sand was plotted, the results were not

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240 significant (R = -0.02, *p* = 0.87) therefore the effect of albedo of the sand of Zeelandia beach

241 was excluded from subsequent analysis.

242

243   3.4. **Incubation temperatures and primary sex ratios**

244   A multiple stepwise regression reveals a strong relationship between air

245 temperature and sand temperature (Multiple R^2 = 0.60, $F_{1,75}$ = 113.2, *p* < 0.001) (Figure 4).

246 Addition of sea surface temperatures to the model only marginally improves the regression

247 (Multiple R^2 = 0.62, $F_{2,74}$ = 60.11, *p* < 0.001). An ANOVA comparing a model with sea

248 surface temperatures to one without sea surface temperatures revealed that the models are

249 not significantly different (*p* = 0.07) and so sea surface temperatures were not included in

250 the model. Additionally, there was no significant effect of depth on sand temperature (*p* =

251 0.84) for the permanent (i.e. non-roving) loggers and so all loggers were pooled together.

252 This lack of a depth cooling effect in the permanent loggers, most probably reflects that they

253 were deployed over a much more restricted depth range than the roving loggers.

254   Using the relationship between air temperature and sand temperature (Figure 4),

255 sand temperatures since the late 1800s were reconstructed. A value of 0.5 °C representing

256 metabolic heating was then added to recreate incubation temperatures. This value is in line

257 with values reported at nesting sites across the world (Howard et al., 2014). Figure 5 shows

258 the mean monthly incubation temperatures based on the ICOADS historical (1823-2014) air

259 temperature data. Mean incubation temperature exceeded the pivotal temperature of 29 °C

260 during the entire nesting season duration so that the emerging hatchling population is

261 predominantly female-skewed, with some seasonal variation due to the variance in mean

262 temperature (Figure 6a). Mean temperatures do not exceed thermal tolerance of 35 °C

263 (Ackerman, 1997) during the hottest period of the year and were used to predict sex ratios

264 indicating an extremely high percentage of female clutches during the nesting season, from

265 40% female in February to >90% in June-November (Figure 6b).

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266   Projecting this model into the future, it is possible to estimate how incubation

267 temperatures are likely to progress. It is estimated that mean incubation temperatures on

268 Zeelandia beach will reach 32.1 °C by the year 2030, 33.0 °C by the year 2060, and 34.2 °C by

269 the year 2090 (Figure 5).

270

271   3.5. **Primary sex ratios**

272   Past sex ratios for Zeelandia beach were reconstructed using the relationship

273 between incubation temperature and primary sex ratios described in 2014 (Laloë et al.

274 2014). No clear trend is visible for the reconstructed data with female production oscillating

275 around 85.9-93.5% across species since the late 1800s (Figure 7). Primary sex ratios have

276 thus been historically female-biased for all three nesting species. When projecting into the

277 future, warming air temperatures will exacerbate this female-bias: female sex ratios are

278 projected to consistently reach >95% after the year 2045 for hawksbills and after 2028 for

279 leatherbacks. It is likely that green turtle sex ratios have already been >95% since 2009.

280

281   **3.6. Nesting surveys and hatching success**

282   Results from surveys from an 11-year period (2002-2012) indicate a small nesting

283 population on Zeelandia beach. Total nest numbers (probable and confirmed) were 255

284 (greens), 104 (hawksbills) and 100 (leatherbacks) for the 11-year period (JB, NE, STENAPA

285 unpublished data). Emergence results were highly variable for greens (42.5 ± 38.3%, n = 68),

286 hawksbills (38.3 ± 38.8%, n = 17) and leatherbacks (11.3 ± 19.4%, n = 50).

287   The incubation temperatures for all recorded nests were reconstructed to study the

288 relationship between incubation temperature and emergence success (Figure 8). There was

289 no clear effect of temperature on emergence success. A large number of nests laid in the

290 northern sector of Zeelandia beach are close to a rainwater gully and several were found to

291 be flooded during excavation (JB, NE, STENAPA unpublished data), possibly explaining the

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292   high number of nests with 0-40% emergence.

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294   **4. Discussion**

295   Mean sand temperatures recorded at the study site were relatively high (29.1-33.3

296   °C) compared to other nesting beaches around the World. For example, mean sand

297   temperatures at nest depths during nesting season were 29.0-31.0 °C in North Carolina, USA

298   (De Gregorio and Southwood Williard, 2011), 29.5 and 32.2 °C for light and dark-coloured

299   beaches respectively at Ascension Island (central Atlantic) (Godley et al., 2002); 30.3-32.4 °C

300   in Barbados (Caribbean) (Horrocks and Scott, 1991); 29.5-33.2 °C in Greece (Mediterranean)

301   (Godley et al., 2001); and 26.7-32.1 °C in Turkey (Kaska et al., 2006). There are few nesting

302   beaches where sand temperatures are below 29 °C, including Queensland, Australia (Wood

303   et al., 2014), southern Brazil (Baptistotte et al., 1999) and Huon Coast in Papua New Guinea

304   (Steckenreuter et al., 2010). This finding of important differences in incubation temperatures

305   around the World has also been made before (Hays et al., 2014) and implies that

306   management plans to aid sea turtle conservation in a warming world need to be regionally

307   tuned.

308   As in this study, female-biased primary sex ratios are being reported at other nesting

309   grounds around the globe (e.g. Barbados, Caribbean; Cyprus, Mediterranean). At some sites

310   female sex ratios as high as 100% are reported (Binckley et al., 1998; De Gregorio and

311   Southwood Williard, 2011). Male-producing beaches still exist but seem to be the exception

312   (Maulaney et al., 2012; Steckenreuter et al., 2010; Stubbs et al., 2014). Our research at a

313   female-biased turtle colony goes one step further by projecting how these sex ratios will

314   progress in the future. Results project the entire feminization of the three sea turtle

315   populations in St Eustatius due to increased air temperatures within the next century.

316   Interestingly, results showed that all three populations have been historically strongly

317   female-biased (Figure 7) and this consistency across species supports the suggestion (Hays et

318   al., 2014) that female hatchling skews may be adaptive. For example sea turtles are

319   polygynandrous a male will mate with more than one female during a breeding season and

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320 females have the capacity to store sperm, which means that a female needs to mate with

321 only one male to fertilise multiple clutches (Pearse and Avise, 2001). As such, an excess of

322 females may be beneficial as it increases the number of clutches of eggs that can be laid in a

323 season. Furthermore, males breed more frequently than females so that female-biased sex

324 ratios translate to more balanced operational sex ratios (Hays et al., 2014). Taken together

325 these findings suggest that female-biased primary sex ratios may be adaptive as they

326 increase the population's natural growth rate (Laloë et al., 2014). In the long term, however,

327 an extremely male-depleted population may not be viable. In this way, understanding how

328 population dynamics are structured by primary sex ratios becomes an important

329 conservation concern.

330 Despite considering a suite of environmental variables for the model, the most

331 robust model put forth is one that only uses air temperature as a predictor variable for sand

332 temperature. Sea surface temperatures were shown to be a good predictor of sand

333 temperature in Northern Australia (Fuentes et al., 2009b) but addition of this variable to the

334 model did not improve the output. On the other hand, similar relationships between air

335 temperature and sand temperature were found at other sites across the world and were

336 shown to be robust and informative (e.g. Hawkes et al., 2007; Laloë et al., 2014; Santidrián

337 Tomillo et al., 2015). It was also shown that rainfall plays an important role in cooling sand

338 temperatures, although it is not a useful predictor variable. This is likely due to the fact that

339 rainfall events are inconstant throughout the nesting season and only have short-term

340 cooling effects on sand temperatures.

341 It was already shown that protracted rainfall has a cooling effect on leatherback

342 nests in Grenada and thus rainfall may allow for the production of more males in the

343 Caribbean (Houghton et al., 2007). In addition to rainfall, this study demonstrates that tides

344 with high coefficients are also important because they can affect the temperature of entire

345 clutches of eggs. This may be the first time such a result has been reported in the literature.

The implications of increased exposure of turtle nests to water (both from rainfall and spring tides) are two-sided: on one hand such events have the potential to cool nests and bring them both below the lethal thermal ranges for development and/or in the male producing thermal range. On the other hand, increased exposure to water can be detrimental to the incubating eggs as a strong negative correlation between sand water content and emergence success exists (Patino-Martinez et al., 2014). Furthermore, an excess of water above a nest can prevent gas exchanges between the air and the nest and asphyxiate the nest (Yalçin-Özdilek et al., 2007). This may be the variable causing a high mortality of nests at the study site. Recording rainfall and sea level rise thus become a conservation priority.

There are certain limitations to the model. For the purpose of succinctness the analysis focussed on scenario A2 in this article. This scenario is commonly used in studies (e.g. Christensen and Christensen, 2003; Wiens et al., 2009). If other SRES scenarios are considered, the overarching results and conclusions are likely to be the same but with varying degrees of urgency. As climate models are further reassessed and refined in the future, so will the ability to assess sea turtle population trends. There are also a suite of assumptions made in the model, including a pivotal temperature of 29 °C. Again, as more information about site-specific parameters are brought forward, the model can be further refined but, in the meantime, the general trends illustrated in the study are likely to hold true.

An important conservation concern is to assess whether or not species can adapt in the face of climate change. Results from this study hint towards potential phenological adaptation. The different turtle species at the study site are affected to varying degrees due to differences in breeding seasons (Figure 6a). Hawksbill turtles have the lowest female sex ratios since these turtles nest ten months each year, during both warm and cool seasons. On the other hand, leatherbacks that nest during the warmest months of the year have the most female-biased sex ratios of the three species. It is theoretically possible that by

372   adjusting their nesting phenology with earlier or later nesting in cooler months, turtles

373   would be able to maintain high female-biased sex ratios and low hatchling mortality rates.

374   Nest depth may only play a limited role in controlling nest temperature at the current

375   nesting depths. Yet since sand temperatures are cooler at extreme depths, if turtles are able

376   to pick up on thermal cues of the sand and dig deeper nests, this would help produce viable

377   nests even as the global temperatures warm. This is potentially an important research

378   question to consider and merits more attention.

379   Not surprisingly, nest depth is coupled with female size (Horne et al., 2014) and

380   reduced survivorship of clutches at shallower depths from smaller adult females may lead to

381   an evolutionary shift towards larger turtles in future generations. Though, this may be

382   obscured by the fact that higher incubation temperatures produce smaller turtle hatchlings

383   (Burgess et al., 2006). In light of these results indicating the current feminisation of the turtle

384   population and that temperature conditions will prohibit successful incubation of turtle

385   nests at Zeelandia beach within 100 years, management practices at this site, and similar

386   sites, may consider adaptations of nest relocation protocols. Adaptations may include

387   relocation to deeper nests, for example, a nest at 100 cm depth is >1 °C cooler than the

388   mean nest depth at Zeelandia beach; this depth is at the extreme end of the range of

389   successful emergences from *in situ* nests as recorded at our study site. Another

390   management strategy at some beaches is shading of surface sand by planting trees along the

391   beach which may decrease temperatures as much as 1.8 °C (Wood et al., 2014).

392   The importance of modelling the effect of increased temperature on hatchling

393   emergence successes is already suggested (Saba et al., 2014; Santidrián Tomillo et al., 2012,

394   2014, 2015). These studies show that warming temperature causes a reduction in female

395   hatchling output due to decrease of hatching and emergence successes. Unfortunately the

396   results presented in this paper regarding hatching success were inconclusive. Hatchling

397   mortality in the face of climate change is an important question that warrants more

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398   attention. Until recently researchers focussed their efforts on understanding the relationship

399   between incubation temperatures and sex ratios (Hawkes et al., 2009). Identifying the

400   pivotal temperature for which both males and females are produced was a research priority

401   (Howard et al., 2014) but now it is necessary to move beyond this and focus on the negative

402   effects of high incubation temperatures, not limiting further research to the study of primary

403   and operational sex ratios, but also to the study of hatchling mortalities. Only then will a

404   holistic model assessing population viabilities be possible.

405   The results from this study underline the threats of climate change to sea turtle

406   populations and highlight the extinction risks of climate change to species whose biology

407   and phenology are closely linked to temperature. For sea turtles, increasing air temperatures

408   has two effects: on one hand it will create female-biased sex ratios, and on the other hand it

409   will increase temperature-linked hatching mortality.

410   This study demonstrates the need to study hatchling mortalities in relationship to

411   increased incubation temperatures, highlights the importance of recording sand

412   temperatures at varying depths, and demonstrates the usefulness of monitoring sand

413   temperatures year-round to assess the potential that sea turtles have for phenological

414   adaptations. Furthermore, investigation of mitigation measures to decrease incubation

415   temperatures is recommended in order to increase survival of sea turtles at sites with high

416   incubation temperatures.

417

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427

428 **Author contributions**

429   NE and GCH conceived the study, NE led the fieldwork with assistance from JB, J-OL

430 led the data analysis with contributions from all authors, all authors contributed to the

431 writing.

432

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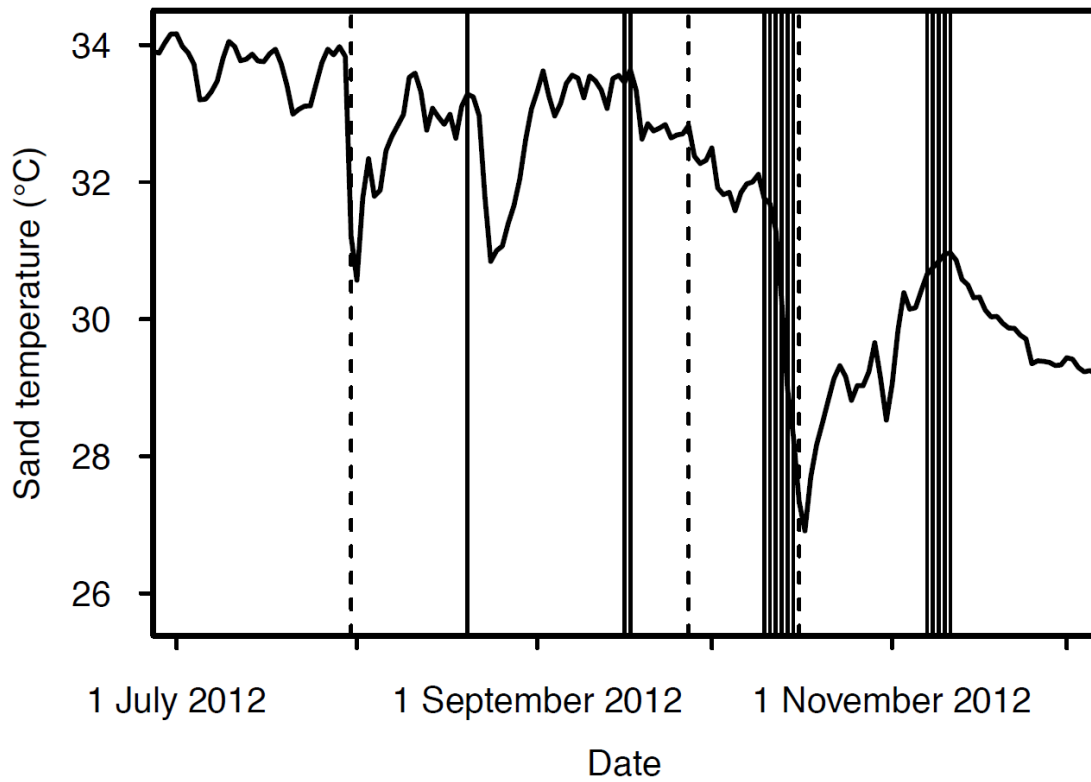551   Res. 23(6), 1379-1390.
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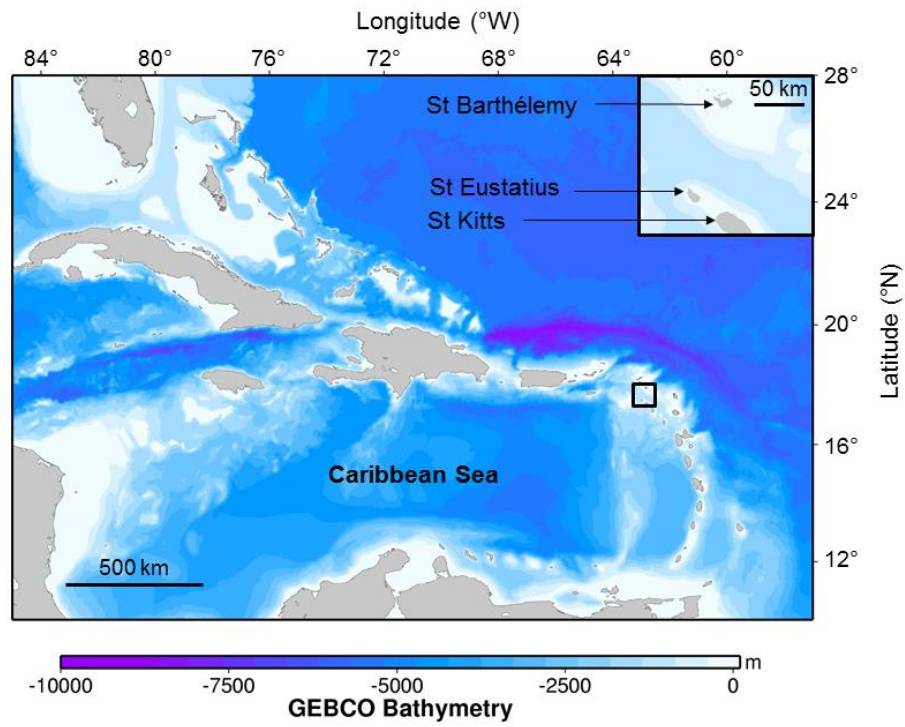
Figure 1:   **Location of St Eustatius in the Lesser Antilles in the north-eastern**

**Caribbean.** The study site, Zeelandia beach, is located on the eastern coast of St Eustatius.

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Figure 2: Rainfall and spring tides have a short-term cooling effect on sand temperature in St Eustatius. The vertical solid lines identify days for which daily precipitation is greater than 10 mm. The dotted lines identify days for which high tide predictions are greater than 50 cm (height above datum). Rainfall and spring tides can be associated to temperature drops, either together or independently, but not all cooling events are associated with one or the other.

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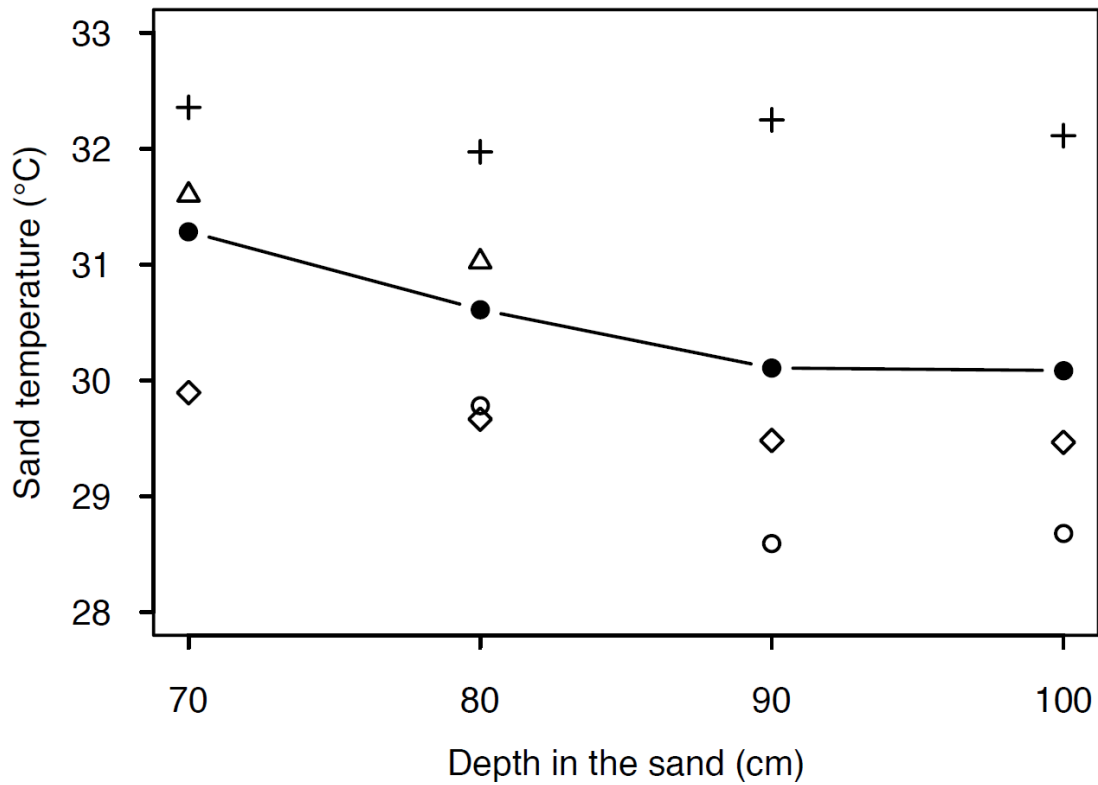
Figure 3: General pattern of decreasing sand temperature with increasing depth. Each

point represents the mean temperature for the duration that the logger was deployed at

each depth: April (◊), June (+), August (Δ), November (o). The studied months cover the

incubation periods for leatherbacks (April, June), greens and hawksbills (June, August,

November). The filled circles represent the mean for each depth. These depths correspond

to the range of nesting depths at this site.

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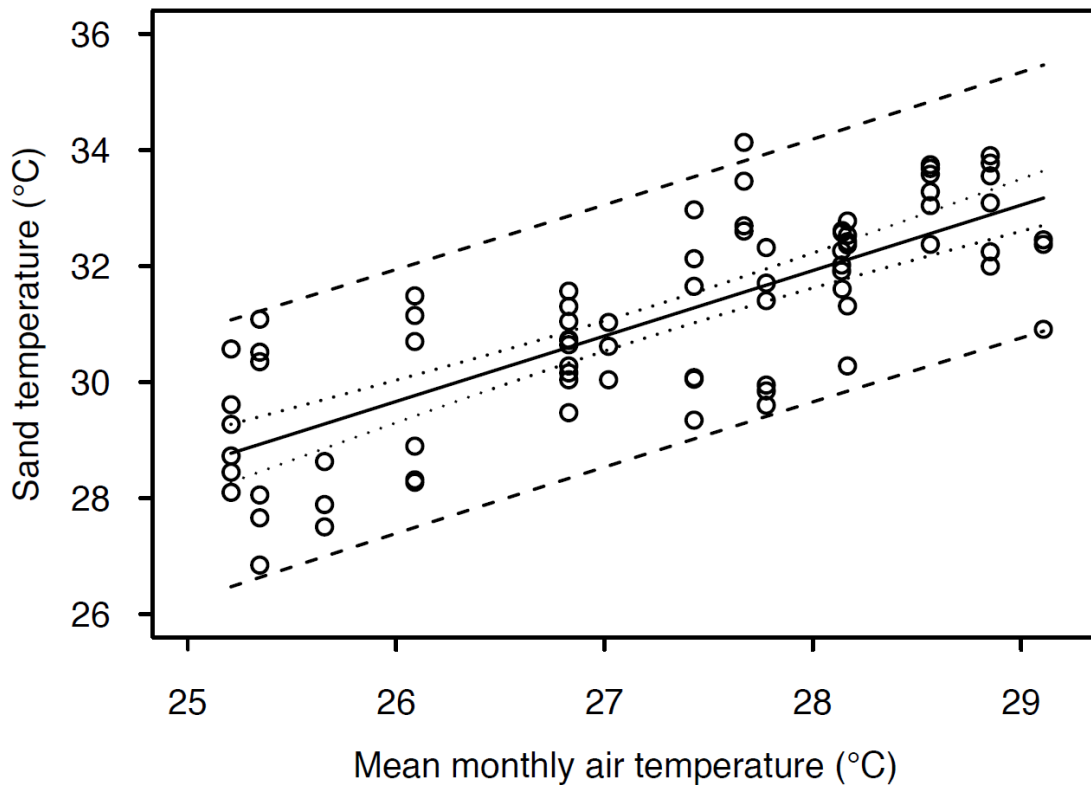
Figure 4: Mean sand temperature (44.6 – 63.3 cm depth range) against mean (monthly) air

temperature for St Eustatius. A single point represents a monthly mean sand temperature

recorded in 2011, 2012 or 2013. The solid line is the regression line, the dotted lines define

the 95% confidence intervals, and the dashed lines define the 95% prediction intervals. The

least squares fit regression equation is: mean sand temperature = 1.13 x air temperature +

0.33 (R^2 = 0.60).
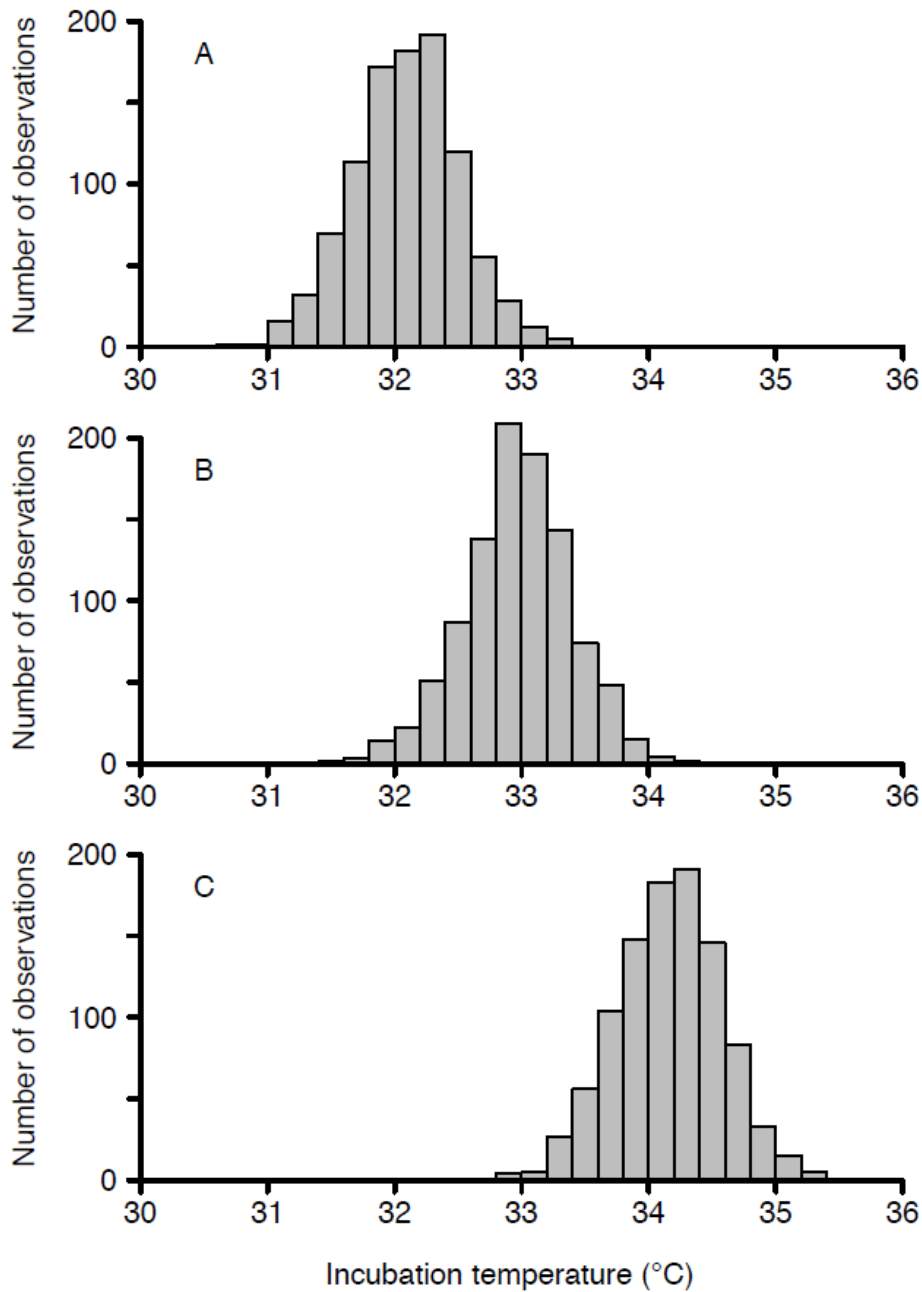
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579 **Figure 5: Projection of incubation temperatures for Zeelandia beach.** A projected increase

580 of air temperatures at the study site will result in an increase of incubation temperatures.

581 Predicted incubation temperatures were estimated for 1000 nests in 2030 (A), 2060 (B), and

582 2090 (C).
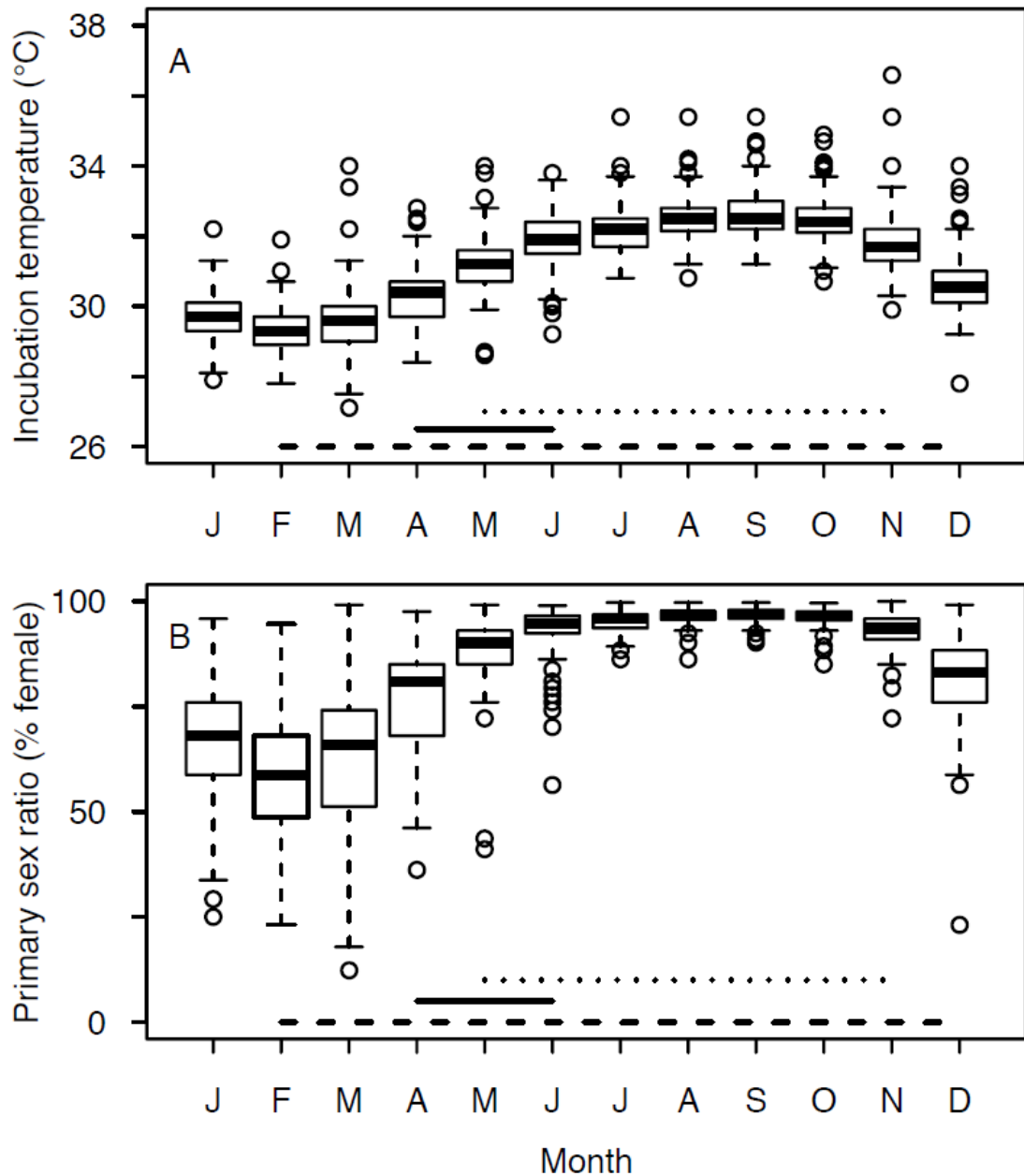
**Figure 6: (A) Seasonality of incubation temperatures at Zeelandia beach and (B) resulting sex ratios.** Historical (1823-2014) air temperatures were used to reconstruct the mean monthly incubation temperatures across this 90-year period. The boxes delineate the upper and lower quartiles and the whiskers define the data's range. Outliers are plotted as separate points. The horizontal lines define the 2012 nesting seasons for each of the three turtle species nesting on St Eustatius: greens (dotted line), hawksbills (dashed line), and leatherbacks (solid line).
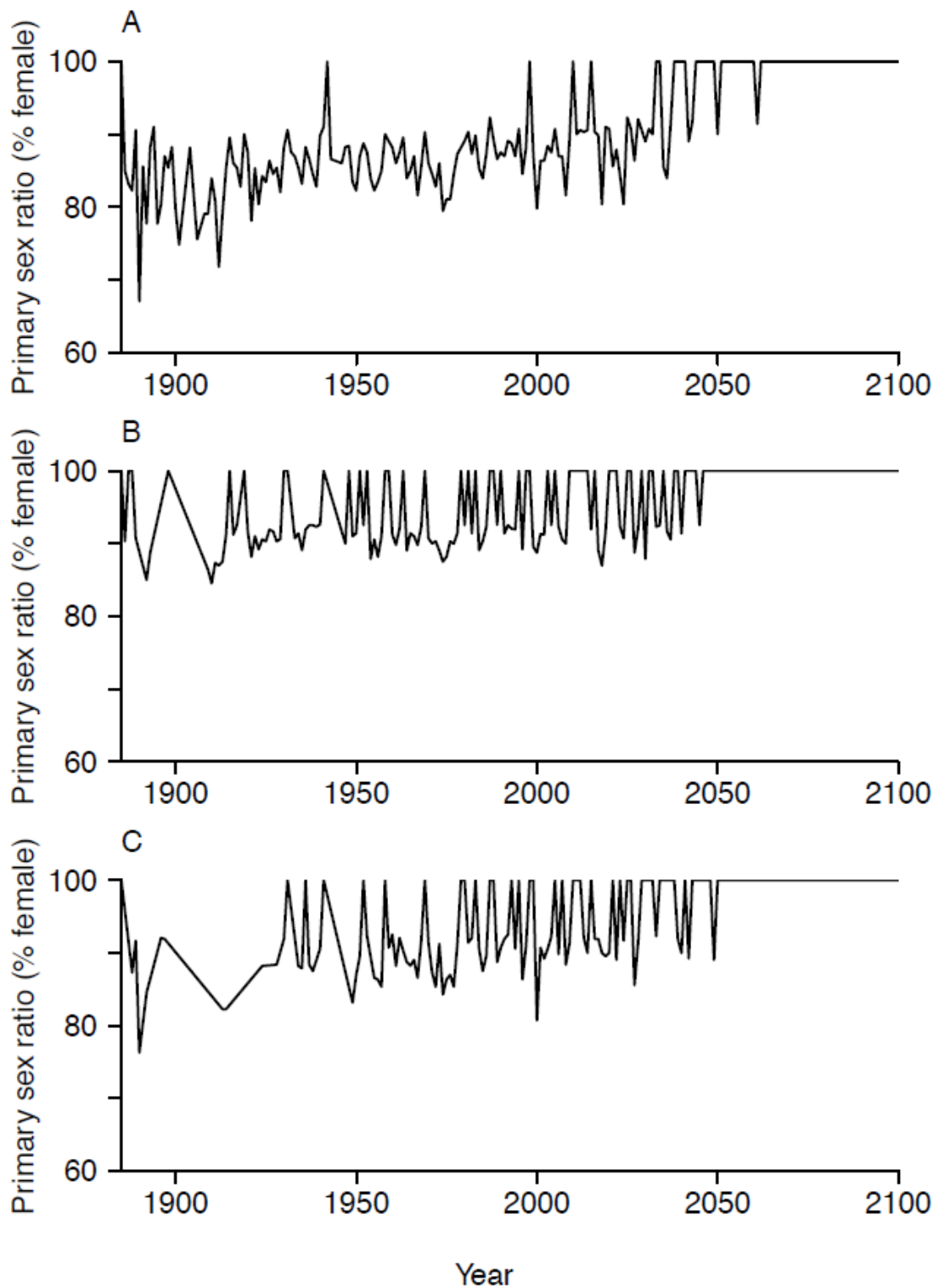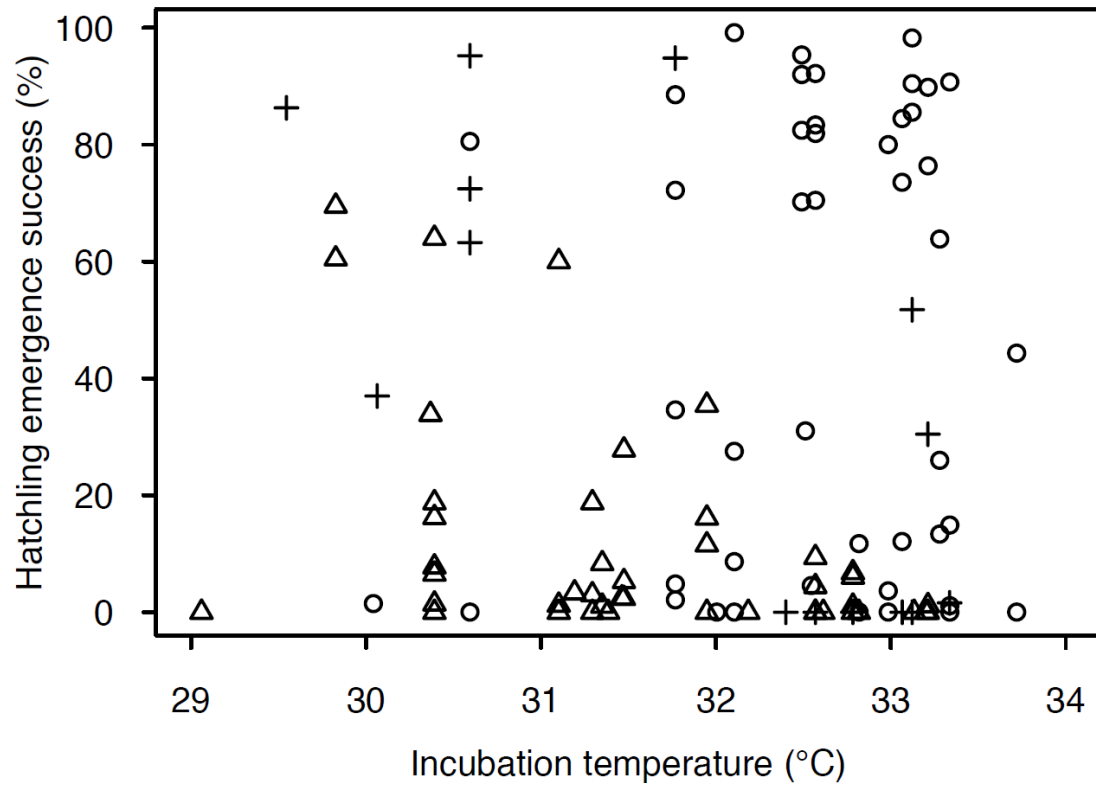
Figure 7: Primary sex ratio reconstruction and projections. Female sex ratios were reconstructed and projected as described in the text for green (A), hawksbill (B), and leatherback turtles (C). Each time-series takes into account the specific nesting season of each species, which explains the differences between time-series.

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Figure 8: Emergence success against incubation temperature. There is no clear effect of
incubation temperature on emergence success for green (o), hawksbill (+), and leatherback
turtles (Δ) at the study site. Most nests fall into two categories: >60% emerged or <40%
emerged.

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