

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/291328999>

# 2016 Marcovaldi JEMBE

DATASET · JANUARY 2016

---

READS

42

## 11 AUTHORS, INCLUDING:



[Milagros López-Mendilaharsu](#)

Tamar-ICMBio

24 PUBLICATIONS 396 CITATIONS

[SEE PROFILE](#)



[Matthew Godfrey](#)

Duke University

100 PUBLICATIONS 2,566 CITATIONS

[SEE PROFILE](#)



[João Carlos A. Thomé](#)

Instituto Chico Mendes de Conservação da ...

11 PUBLICATIONS 153 CITATIONS

[SEE PROFILE](#)

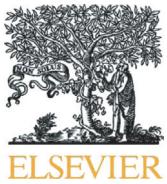


[Mariana M. P. B Fuentes](#)

Florida State University

38 PUBLICATIONS 424 CITATIONS

[SEE PROFILE](#)



## Identification of loggerhead male producing beaches in the south Atlantic: Implications for conservation



Maria A.G.dei Marcovaldi <sup>a,1</sup>, Milagros López-Mendilaharsu <sup>a</sup>, Alexsandro S. Santos <sup>a</sup>, Gustave G. Lopez <sup>a</sup>, Matthew H. Godfrey <sup>b</sup>, Frederico Tognin <sup>a</sup>, Cecília Baptista <sup>c</sup>, Joao C. Thomé <sup>c</sup>, Augusto C.C. Dias <sup>c</sup>, Jaqueline C. de Castilhos <sup>c</sup>, Mariana M.P.B. Fuentes <sup>d,\*1</sup>

<sup>a</sup> Fundação Pró Tamar, Rua Rubens Guelli, 134 sala 307, Salvador, Bahia, Brazil

<sup>b</sup> North Carolina Wildlife Resources Commission, Beaufort, NC, United States

<sup>c</sup> Centro Tamar/ICMBio, Av. Nossa Senhora das Navegantes, 700-A – Vitória, Espírito Santo, Brazil

<sup>d</sup> Department of Earth, Ocean and Atmospheric Science, Florida State University, Tallahassee, FL, United States

### ARTICLE INFO

#### Article history:

Received 29 July 2015

Received in revised form 3 January 2016

Accepted 4 January 2016

Available online xxxx

#### Keywords:

Sea turtles

Climate change

Loggerhead turtles

Sex ratio

Incubation duration

Brazil

### ABSTRACT

Concern over the potential impacts of increased temperature on marine turtles, which have temperature dependent sex determination, has resulted in an increase in research that predicts the sex ratio of marine turtle hatchlings under various scenarios of climate change. To accurately understand the projected impacts from global warming, it is necessary to understand the sex ratio baseline in advance of climate change. To address this, the primary sex ratio of loggerhead hatchlings, *Caretta caretta*, was estimated from incubation duration of 27,697 *in situ* nests from 21 nesting beaches used by two subpopulations of loggerhead turtles in Brazil over the last 25 years. A strong female bias (94%) was observed in all the areas used by the northern loggerhead stock, Sergipe (SE) and Bahia (BA), whereas a more balanced sex ratio (53% female) was estimated at the regions used by the southern loggerhead stock, Espírito Santo (ES) and Rio de Janeiro (RJ). Both inter-annual (SE: 83% to 99%; BA: 79% to 98%; ES: 33% to 81%; RJ: 18% to 81%) and inter-beach variabilities (SE: 91% to 98%; BA: 89% to 96%; ES: 47% to 69%; RJ: 28% to 55%) in mean female offspring were observed. These findings provide evidence of persistent female bias in Brazil, and importantly identify male producing beaches and months, which will guide management decisions.

© 2016 Elsevier B.V. All rights reserved.

## 1. Introduction

Animals with temperature dependent sexual determination (TSD), in which their sex is determined by temperature during embryonic development, are predicted to experience an extreme sex ratio bias from projected global warming ([Fuentes et al., 2010](#); [Janzen, 1994](#); [Mitchell and Janzen, 2010](#)). A forced alteration in sex ratio can have major implication to reproductive factors, and may reduce rates of fertilization and loss of genetic variation impacting the viability of populations ([Fuller et al., 2013](#); [Wibbels, 2003](#)). For example, marine turtles exhibit TSD, where warmer incubation temperatures yield a higher proportion of female hatchlings ([Mrosovsky and Yntema, 1980](#)). Thus, projected increases in sand temperature during nesting seasons are predicted to skew marine turtle populations towards predominantly females ([Fuentes and Porter, 2013](#); [Hawkes et al., 2007](#)).

Concerns over the potential feminization of marine turtle populations from global warming has resulted in an increase in research that

predicts the sex ratios of marine turtle hatchlings under various scenarios of climate change ([see\(Hamann et al., 2013; Hawkes et al., 2009\)](#)). However, to accurately understand the projected impacts from global warming, it is necessary to understand the sex ratio baseline in advance of climate change ([Marcovaldi et al., 2014; Zbinden et al., 2007](#)). There are challenges to establishing baselines datasets on marine turtle hatchling sex ratios. Specifically, difficulties associated in classifying the sex of marine turtle hatchlings (e.g., lack of sexually dimorphic external characteristics), result in datasets with limited spatio-temporal scales that hamper a deeper understanding of the variability of offspring sex ratios within and between seasons and nesting grounds at a population scale ([Fuller et al., 2013; Godfrey and Mrosovsky, 1999](#)). Indeed, the need for sex ratio estimates across multiple years and from multiple beaches within the range of a marine turtle population has been highlighted by recent studies ([Fuller et al., 2013; Marcovaldi et al., 2014](#)).

Most of the studies on the sex ratios of marine turtle hatchlings has been conducted for the loggerhead turtle, *Caretta caretta* ([Fuller et al., 2013; Hawkes et al., 2009; Witt et al., 2010](#)), with the majority reporting a female bias (e.g.,[\(Fuller et al., 2013; Godley et al., 2001a; Marcovaldi et al., 1997\)](#) for a summary review see S1 Table and ([Hays et al., 2014](#))

\* Corresponding author.

E-mail address: [mfuentes@fsu.edu](mailto:mfuentes@fsu.edu) (M.M.P.B. Fuentes).

<sup>1</sup> These authors contributed equally to this work.

and only a few reporting male producing beaches ([Baptistotte et al., 1999](#); [Foley et al., 2000](#); [Iribi and Bradai, 2014](#); [Margaritoulis, 2005](#); [Schmid et al., 2008](#)). Most of the studies conducted to date have been based on data for a small spatial range (1 or 2 beaches) and short-temporal scales (1 or 2 nesting seasons) ([Fuller et al., 2013](#)), with a few studies undertaken over a larger temporal scale (6 to 26 years) (see – [Fig. 1](#), S1 Table) and one study that reconstructed past sex ratios to the 1850s using climate proxies ([Laloe et al., 2014](#)). Although long term studies provide the appropriate temporal scale to discern overall trends in sex ratios, many of them are outdated, with data from 2009 or earlier, and only a few studies provide sex ratio data after 2010 ([Fig. 1](#), S1 Table). The lack of studies during the last decade is of concern as there is no information on whether the biased sex ratios found from 1970 to 2009 at loggerhead nesting grounds have changed over recent time and whether hatchling production has become completely feminized.

To address these knowledge gaps and explore whether the sex ratio of loggerhead turtles at important nesting areas has changed over the last decade, an earlier study that estimated the sex ratio of loggerhead hatchlings from *in situ* nests from 11 nesting beaches in Brazil from 1988 to 1994 was expanded (see [Marcovaldi et al., 1997](#)). In addition to expanding the temporal scale of the analysis to 25 nesting seasons (1989/90–2013/14), including the last decade, the spatial range (21 nesting beaches, across 612 km), including beaches in Rio de Janeiro, which encompasses the southern range of loggerhead nesting in Brazil, was expanded covering the nesting area of two subpopulations of loggerhead turtles ([Reis et al., 2010](#)). To better inform future assessments of impacts of climate change on these two subpopulations, the variability of sex ratio produced between nesting beaches and years were explored.

## 2. Material and methods

### 2.1. Study species and location

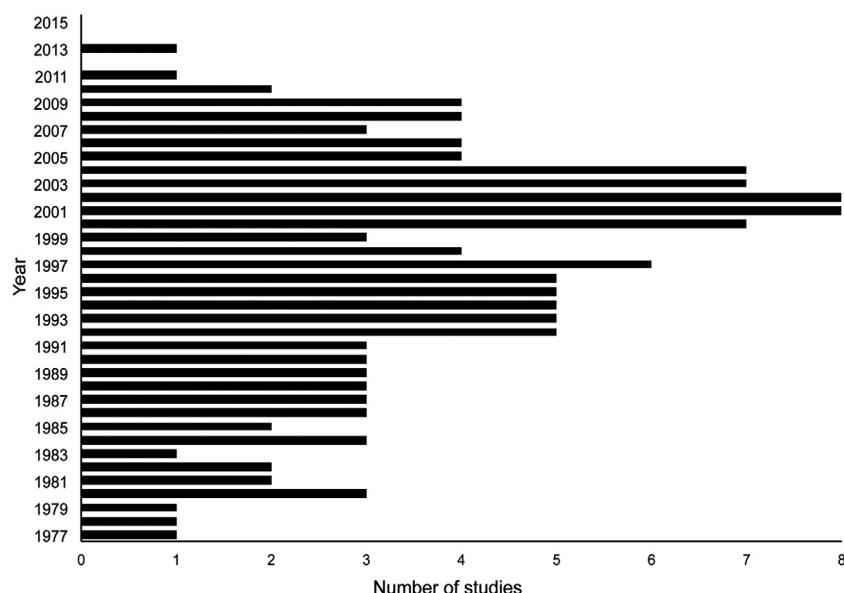
The work was conducted at the extent of nesting areas used by the Brazilian loggerhead genetic stock resident in south Atlantic waters ([Fig. 2](#)) ([Marcovaldi and Chaloupka, 2007](#)), which occur across 4 regions: Sergipe (SE), Bahia (BA), Espírito Santo (ES) and Rio de Janeiro (RJ) ([Fig. 2](#)) ([Marcovaldi and Chaloupka, 2007](#)). Nesting grounds in this region are part of the Southwest Atlantic loggerhead Regional

Management Unit (RMU) ([Wallace et al., 2010](#)). Two genetically distinct populations are observed in Brazil; the northern stock (SE and BA) and the southern stock (ES and RJ) ([Reis et al., 2010](#)). Within each stock the northern coast of the state of Bahia and Espírito Santo have the majority (75%) of loggerhead nesting in Brazil ([Marcovaldi and Chaloupka, 2007](#); [Marcovaldi and de Marcovaldi, 1999](#)). Nesting activity occurs from September to March, with a peak in November and December ([Lima et al., 2012](#); [Marcovaldi and Chaloupka, 2007](#)).

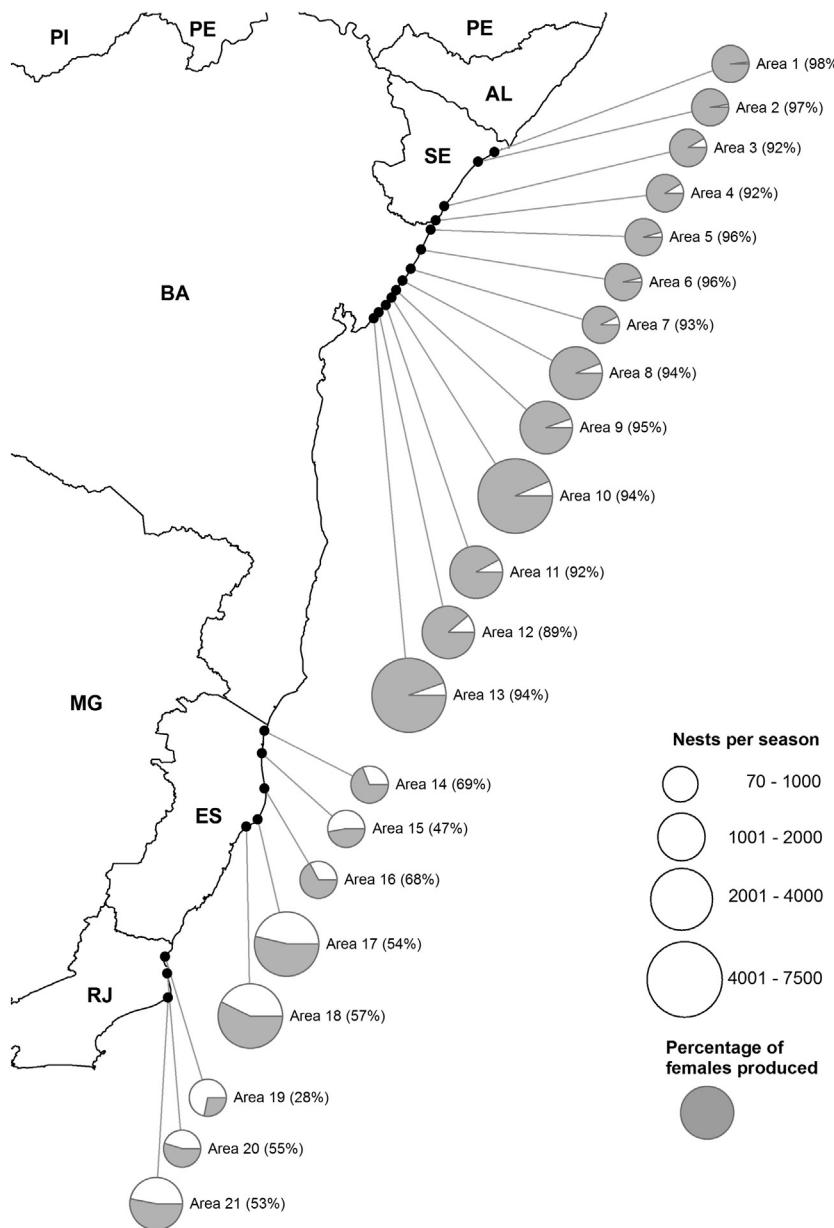
Data on incubation durations of loggerhead nests were collected from 21 nesting areas (SE = 3, BA = 10, ES = 5 and RJ = 3) ([Fig. 2](#) and [Table 1](#)), beach descriptions can be found in [Baptistotte et al. \(1999\)](#), [Marcovaldi et al. \(2007\)](#) and [Lima et al. \(2012\)](#) (see [Baptistotte et al., 1999](#); [Lima et al., 2012](#); [Marcovaldi and Chaloupka, 2007](#)). Nesting areas were selected based on their importance and distinct characteristics (e.g., sand colour and grain size). All areas are intensive study areas and are patrolled daily during the nesting season by TAMAR staff (for information on TAMAR, see [Marcovaldi and de Marcovaldi, 1999](#)). To protect nests from erosion, predation, and coastal development, TAMAR relocates clutches, that would otherwise not survive, to open air hatcheries and safer locations in the beach ([Marcovaldi and de Marcovaldi, 1999](#); [Naro et al., 1999](#)), this study only considers nests that remained *in situ*. During patrols, all freshly laid nests were marked and monitored during incubation, and excavated the morning after emergence when all eggs were examined to determine species and hatching success. Incubation duration was calculated as the time in days between laying (the date of the morning when a freshly laid nest was first found) and the date of the morning of the first day when hatchling tracks on the sand indicated their emergence from the nest. Incubation periods of less than 45 days were not considered ( $n = 11$ ), since it is uncommon in Brazil to have loggerhead nests incubating for less than 45 days, thus any records with less than 45 days are considered to be an error in data collection. The spatio-temporal scale of available incubation duration data varies across the different regions and areas as a reflection of TAMAR's work in the area (for a summary see [Table 1](#)).

### 2.2. Estimating sex ratios from incubation duration

The relationship between incubation duration and sex ratio was used to convert nest incubation duration ([Table 1](#)) into nest hatchling sex ratio (as per [Fuller et al., 2013](#); [Godley et al., 2001b](#); [Marcovaldi](#)



**Fig. 1.** Number of studies that have explored hatchling sex ratios of loggerhead turtles from 1977 to 2015. The same study was counted for each year that it determined the sex ratio of offspring, so one study could have been counted multiple times.



**Fig. 2.** Study sites with estimated proportion of females (grey) and male (white) loggerhead hatchlings in each area.

et al., 2014). For this, previously derived relationship from constant temperature laboratory experiments for loggerhead turtle eggs from Bahia, Brazil were used (Marcovaldi et al., 1997), where a field pivotal incubation duration of 59.3 days was determined. This includes a correction factor of 4 days for the hatch-emergence interval that occurs in naturally incubating marine turtle nests (see (Godfrey and Mrosovsky, 1999)). To calculate the overall sex ratio for *in situ* nests for each season and year, the number of all clutches *in situ* at half-month periods within the nesting season was taken into account (as per (Godley et al., 2001b; Marcovaldi et al., 1997; Marcovaldi et al., 2014)). As the temporal scale of the incubation dataset varies across the different regions (SE, BA, ES, RJ) and areas (areas 1 to 21), only a subset of the data that encompassed the same temporal scale for all locations was used to compare incubation durations between the different regions and areas. For comparisons across regions data from 2005/2006 to 2012/2013 (8 seasons) for all areas were used, except for areas 14, 15, 16, 19 and 20 because data for those years were unavailable. For comparisons between areas within regions a different subset of data

for each region were used depending on the temporal coverage of each area (see S2 Table).

Some loggerhead nests laid in the study areas are relocated to safer incubation areas, either up the beach or to centralized incubation areas (Marcovaldi and de Marcovaldi, 1999). These relocated nests may experience different thermal conditions during incubation than nests left in place (*in situ* – see (Naro et al., 1999)), thus relocated nests were not included in the study and only *in situ* nests were considered.

### 3. Results

81,132 loggerhead clutches were documented in the study areas during the study period (1989/90–2013/14, as per Table 1). Of these, 53,435 (65%) were relocated to hatcheries or safer locations in the beach and thus not included in the analyses. Incubation duration values were available for 27,697 *in situ* clutches that successfully produced hatchlings (Table 1).

**Table 1**

Incubation duration data on loggerhead turtle nests available from each study location.

Region	Area	Beach	Beach length (km)	Seasons of data	Nesting seasons monitored	Records of nests in situ	Mean incubation duration [range] days	% Female [range]
Sergipe	1	Ponta dos Mangues	36	89/90 to 91/92, 93/94, 01/02 to 03/04, 05/06 to 12/13.	15	106	50 [45–57]	98.11 [99.95–81]
	2	Pirambu	53	89/90 to 91/92, 93/94 to 96/97, 98/99, 99/00, 01/02, 03/04 to 13/14.	21	243	51 [45–71]	97.02 [99.95–0]
	3	Abais	36	89/90, 90/91, 93/94, 94/95, 96/97, 97/98/02/03, 03/04, 05/06 to 12/13.	16	71	52 [46–72]	91.58 [99.92–0]
Total SE Bahia	4	Mangue Seco to coqueiro	125	03/04, 05/06 to 13/14.	10	420	52 [46–79]	95.57
	5	Dunas to Costa Azul	15	04/05 to 13/14.	10	203	51 [45–66]	91.54 [99.92–0]
	6	Siribinha to Ribeiro	23	94/95 to 96/97, 03/04 to 13/14.	14	728	50 [45–77]	95.95 [99.95–4.12]
	7	Baixios to Mamucabó	44	93/94, 97/98, 00/01 to 13/14.	16	902	52 [45–69]	96.19 [99.95–0]
	8	Subauma to Porto do Sauípe	18	93/94, 97/98, 00/01 to 13/14.	18	1029	51 [45–79]	92.63 [99.95–0]
	9	Costa do Sauípe to Imbassai	23	89/90 to 91/92, 94/95, 95/96, 97/98, 02/03 to 13/14.	21	1631	51 [46–71]	94.03 [99.95–0]
	10	Praia do Forte	16	89/90 to 13/14.	25	4259	52 [45–79]	94.52 [99.92–0]
	11	Itacimirim to Barra do Jacuípe	14	01/02 to 13/14.	13	1369	52 [45–80]	93.52 [99.95–0]
	12	Berta to Arembepe	11	90/91 to 13/14.	24	1611	52 [45–72]	91.92 [99.95–0]
	13	Santa Maria to Busca Vida	16	89/90 to 13/14.	25	7514	51 [45–79]	88.88 [99.95–0]
			196			19,666		94.50 [99.95–0]
								93.37
Total BA Espírito Santo	14	Itaunas	31	91/92 to 07/08, 10/11 to 12/13.	20	246	56 [46–80]	68.75 [99.97–0]
	15	Guriri	52	89/90 to 08/09, 10/11 to 13/14.	24	360	60 [45–78]	47.10 [99.97–0]
	16	Pontal do Ipiranga	28	89/90, 90/91, 92/93 to 00/01, 04/05 to 06/07, 12/13.	15	313	56 [45–80]	67.54 [99.97–0]
	17	Povoacão	38	89/90 to 13/14.	25	2005	59 [45–80]	53.77 [99.97–0]
	18	Comboios	37	89/90 to 13/14.	25	2831	58 [45–80]	57.16 [99.97–0]
			186			5755		58.87
Total ES Rio de Janeiro	Area 19	Barra de Itabapoana to Praia do Sul	36	13/14.	1	53	64 [47–79]	28.00 [99.87]
	Area 20	Ilha de Convivência to Açu	38	00/01, 01/02, 04/05, 08/09 to 13/14.	9	335	58 [45–80]	54.57 [99.95–0]
	Area 21	Maria Rosa to Barra do Furado	31	01/02, 03/04 to 13/14.	12	1468	59 [47–80]	52.89 [99.87–0]
			105			1856		45.15
			621			27,697		

### 3.1. Incubation duration

Mean incubation duration increased from north to south, with 96.5% of nests from the northern stock (SE and BA) and 56% of nests from the southern stock (ES and RJ) incubating in less than the pivotal incubation duration (59.3 days, see [Marcovaldi et al., 1997](#)) (Fig. 3), with eggs in ES and RJ generally taking longer to incubate. Incubation duration was significantly different across nesting regions (One-way ANOVA, DF = 15,366, F = 2451, P < 0.05). Incubation duration in Sergipe and Bahia were not significantly different (for the years compared: (SE) range: 45–72, mean: 51 ± 3 SD days; (BA) range: 45–80, mean: 51 ± 3 SD days); whereas the incubation duration in Espírito Santo and Rio de Janeiro was significantly different (for the years compared: (ES) range: 47–80, mean: 59 ± 7 SD days; (RJ) range: 47–80, mean: 60 ± 7 SD days, N = 5755 (ES, 1856 (RJ), Tukey-Kramer HSD post-hoc test, (ES) q = 7.544, q = 6.90, q = −0.98, P < 0.05 and (RJ) q = 8.53, q = 7.88, q = 0.98, P < 0.05).

### 3.2. Comparisons across areas

In SE, Area 3 (Abais) was significantly different to Areas 1 (Ponta dos Mangues) and 2 (Pirambu) (N = 278, Tukey-Kramer HSD post-hoc test, q = 2.5152, q = 2.268, P < 0.05, respectively), and had a longer mean incubation duration (for the years compared: range 46–72, mean 53 ± 5 SD days) (Fig. 3, Table 1). Areas 1 and 2 were not significantly different, with a mean incubation duration of 50 ± 2 SD days; however, for the years compared, Area 1 had a maximum incubation duration of 57 days.

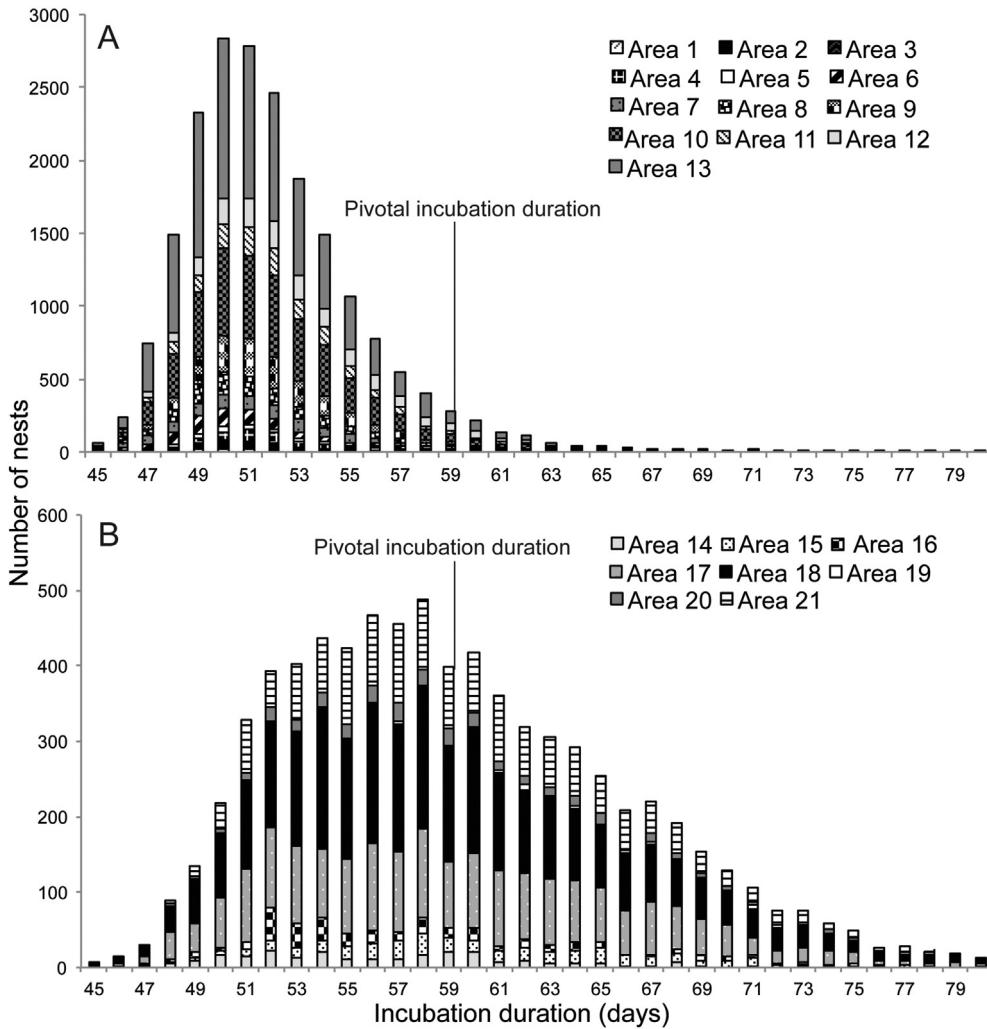
In BA, Areas 6 (Siribinha to Ribeiro) and 12 (Berta to Arembepe) presented the most distinct incubation durations; with Area 6 having

significantly shorter incubation duration than the other Areas in BA, except for Areas 5 (Dunas to Costa Azul), 8 (Subauma to Porto do Sauípe), and 9 (Costa do Sauípe to Imbassai) (Area 6 for the years compared: range 45–77, mean: 50 ± 3 SD days, N = 12,511, Tukey-Kramer HSD post-hoc test, q = −1.89, q = −1.33, q = −1.06, q = −1.798, q = −2.59, q = −0.67, P < 0.05). Area 12 had significantly longer incubation duration than all other nesting areas in BA, except for Area 4 (Mangue Seco) to Area 12 (Coqueiro) (for the years compared: range: 45–72, mean: 53 ± 4 SD days, N = 12,511, Tukey-Kramer HSD post-hoc test, q = 1.68, q = 2.39, q = 1.33, q = 1.48, q = 1.24, q = 1.14, q = 0.67, q = 1.59, P < 0.05) (Fig. 3, Table 1).

In ES, Area 15 (Pontal do Ipiranga) had the most distinct incubation duration with significantly longer incubation duration than any other area in ES, except for Area 17 (Povoacão) (Area 15 for the years compared: range 45–78, mean: 61 ± 6 SD days, N = 2717, Tukey-Kramer HSD post-hoc test, q = 3.06, q = 3.352, q = 1.897, P < 0.05, respectively) (Fig. 3, Table 1). Area 14 (Itaunas) and 16 (Pontal do Ipiranga) had the shortest mean incubation durations in ES (for the years compared: range 46–80, mean: 57 ± 6 SD days and range 45–80, mean: 57 ± 6 SD, respectively).

In RJ, a comparison across areas was only possible for one season (13/14), which indicated that area 19 (Barra de Itabapoana to Praia do Sul) was significantly different to the other two areas in RJ, with a longer mean incubation duration (Area 19 for the year compared: range 47–79, mean: 64 ± 7 SD days, N = 293, Tukey-Kramer HSD post-hoc test, q = 1.280, q = −4.54, P < 0.05) (Fig. 3, Table 1).

No significant increase or decrease was observed with annual mean incubation durations over time for any of the regions (Fig. 4). However, an increase in maximum incubation duration was observed in BA and RJ. In RJ, a decrease in the minimum incubation duration was also observed (Fig. 4).



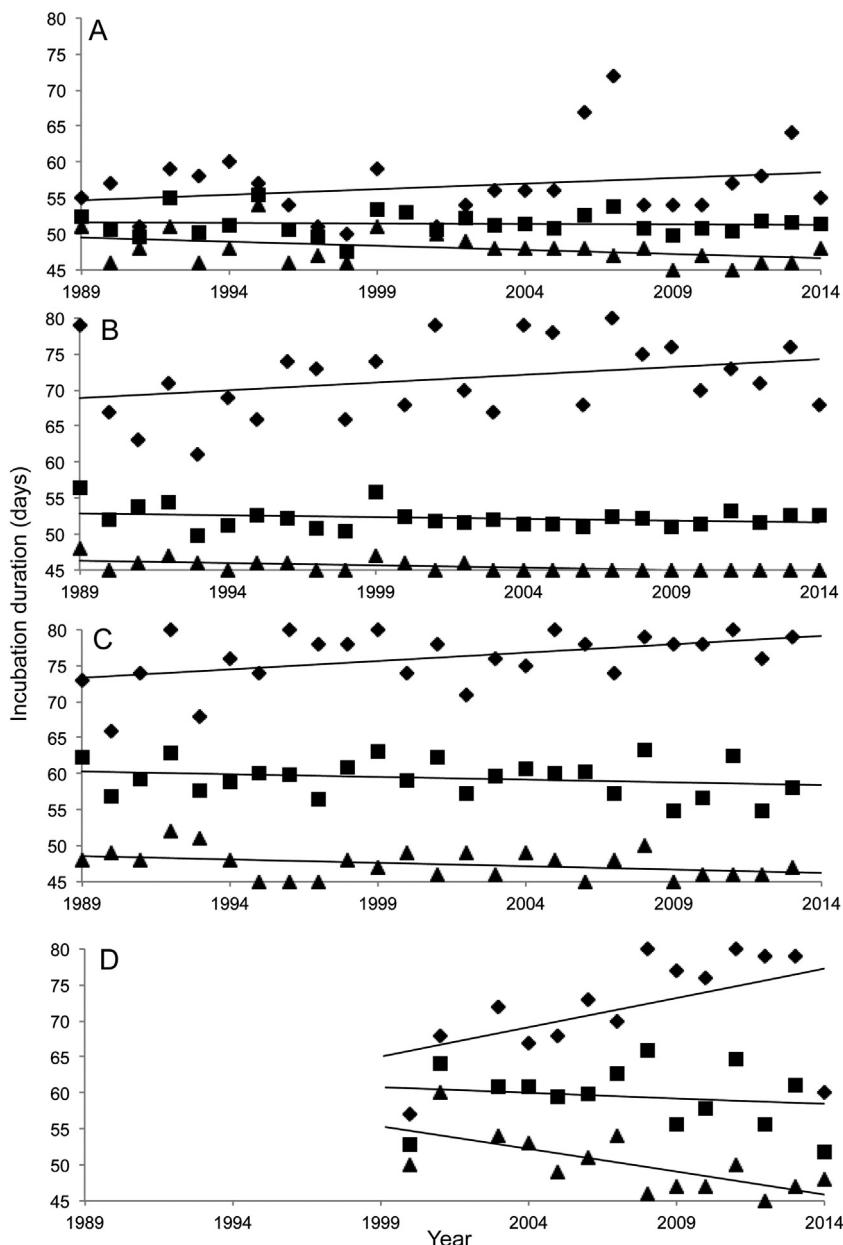
**Fig. 3.** Incubation periods of loggerhead turtle clutches at nesting areas in A) Sergipe and Bahia, northern stock (89–1990–13/2014) and B) Espírito Santo, southern stock (89–90–13/14) and Rio de Janeiro (04/05–13/14).

### 3.3. Sex ratio estimates

Female hatchling production decreased from the northern to the southern regions (SE: mean  $95.57\% \pm 11$ , BA: mean  $93.37\% \pm 15$  SD, ES: mean  $58.87\% \pm 38$  SD, RJ: mean  $45.15\% \text{ females} \pm 38$  SD, Fig. 2). A strong female bias was observed in all the areas used by the northern loggerhead stock, with areas in SE and BA producing a higher proportion of females (88.87% to 98.10%). Areas 1 and 2 in SE produced the highest proportion of females from all the studied areas (97.0% and 98.10% respectively). A more balanced (50:50) sex ratio was estimated at the regions used by the southern loggerhead stock, with areas 15 (Guriri) and 19 (Barra de Itabapoana to Praia do Sul) in ES and RJ respectively, producing a higher proportion of males. Both inter-annual (SE: 82.92% to 99.72%, BA: 78.90% to 98.27%, ES: 33.15% to 81.0%, RJ: 18.51% to 81.40%) and inter-beach variabilities (SE: 91.57% to 98.10%, BA: 88.875 to 96.19%, ES: 47.09% to 68.75%, RJ: 28% to 54.57%, see Table 1, Fig. 2) in mean female sex ratios were observed. Inter-monthly variation in mean offspring sex ratio was also observed (Fig. 5). Overall the southern stock (ES and RJ), produced 47% of male hatchlings, with a higher proportion of male hatchlings being produced from nests laid at the beginning and at the end of the nesting season (September–October and April). The northern stock (SE and BA) produced 6% of male hatchlings, with a higher proportion of males produced from nests laid in August and April–May in BA, when the proportion of nests are low (Fig. 5). In SE a low proportion of males is produced throughout the nesting season (Fig. 5).

### 4. Discussion

Loggerhead nesting beaches in Brazil continue to produce female biased hatchling sex ratios. Female skew was found to be more prominent at beaches used by the northern stock, whereas beaches in the southern stock produced a more balanced sex ratio. The proportion of female offspring decreased from north to south as a reflection of northern beaches experiencing higher sand temperatures. Inter-annual and inter-monthly variations in mean offspring produced were also observed. Inter-annual variability was higher in Rio de Janeiro (18.51% to 81.40%), where an increase in maximum incubation duration and a decrease in the minimum incubation duration were observed in the last 13 years, increasing the range of incubation durations observed over a given season. Several factors could be driving these changes including: 1) bigger fluctuations in sand temperatures during the nesting season and across years, and/or 2) variability in nest site selection, with cooler and warmer areas being selected by females to lay their clutches of eggs (Marcovaldi et al., 2014). Despite higher proportion of females being produced in northern beaches, male clutches are produced by both stocks at some point during the nesting season. Inter-beach variability in the proportion of female offspring produced was a reflection of the proportion of nests being laid before the incubation temperatures started to produce female hatchlings. Nests in the southern stock peaks in months (November–December) when temperatures are cooler compared to the northern stock where nests peaks in months

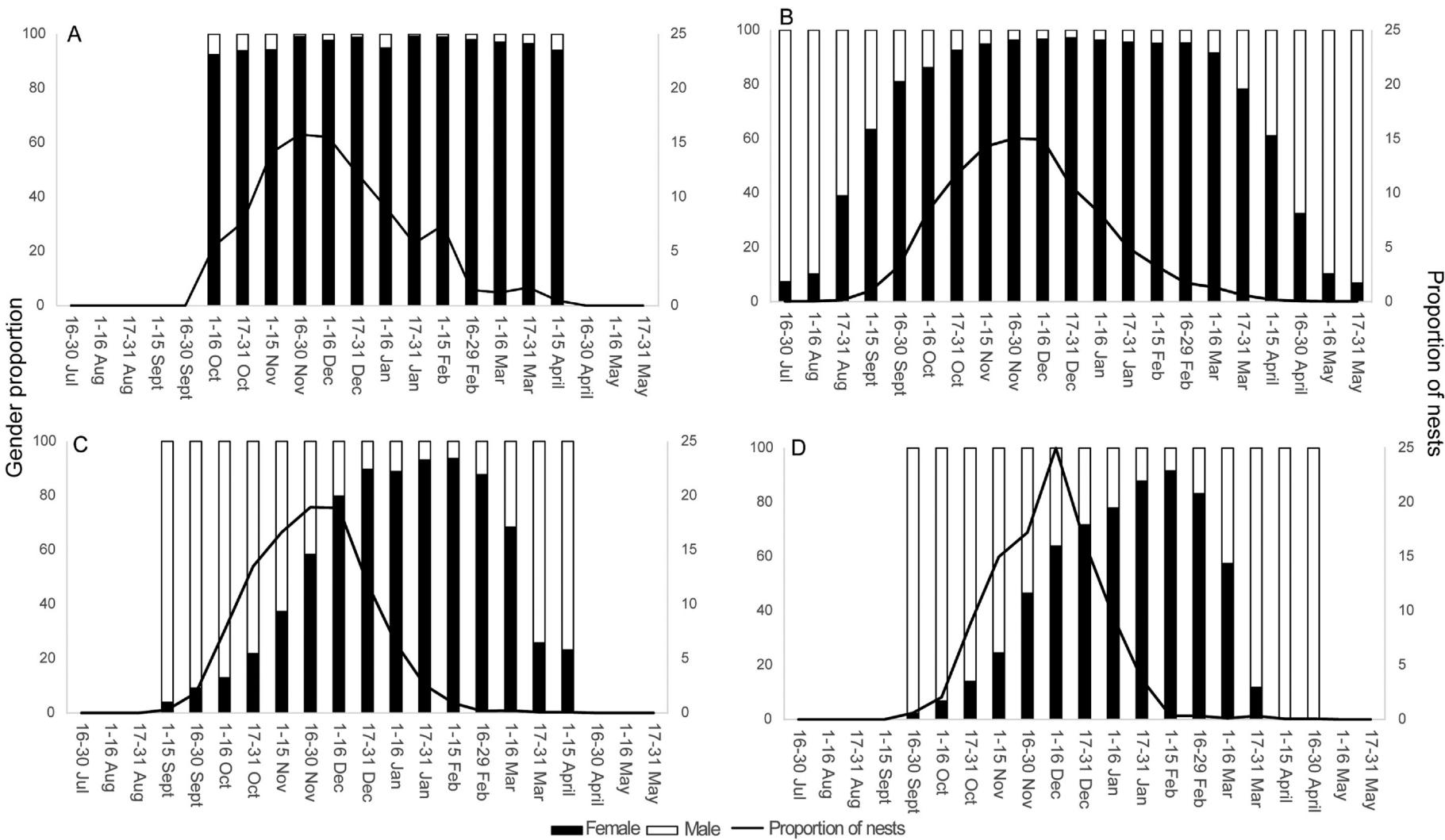


**Fig. 4.** Inter-annual incubation duration of loggerhead clutches in A) Sergipe, B) Bahia, C) Espírito Santo and D) Rio de Janeiro. ▲ Minimum incubation duration, ■ mean incubation duration, and ♦ maximum incubation duration.

(November–January) when temperatures are warmer. The results from this study are consistent with previous work where it was estimated that 82% of hatchlings produced across 11 nesting beaches in SE, BA, and ES from 1989 to 1994 were females (Marcovaldi et al., 1997) and another study that identified male producing sand temperatures in ES (Baptistotte et al., 1999). By exploring offspring sex ratio over a wider spatial (21 nesting beaches comprising 612 km) and temporal scale (25 nesting seasons), and extending the study to include the southern-most nesting areas for the loggerhead population in Brazil, the temporal and spatial trends in sex ratio production were explored to better characterize the sex ratio of hatchlings produced in the whole of Brazil, providing insights into regional and temporal differences. Most importantly, male producing beaches and months were identified. Apart from this study, to date only a few studies have identified loggerhead male producing beaches, which are located in Espírito Santo, Brazil, southwestern Florida, USA, Kuriat islands, Tunisia, Zakynthos Island, Greece, and Heron Island, Australia (Baptistotte

et al., 1999; Foley et al., 2000; Jribi and Bradai, 2014; Limpus et al., 1983; Margaritoulis, 2005; Schmid et al., 2008).

Identifying and improving the protection of male-producing beaches has been highlighted as high priority to mitigate potential impacts from projected increases in temperature on marine turtles (Fuentes et al., 2012; Hawkes et al., 2007). At beaches that produce a majority of female hatchlings, nests laid during male producing months (usually at the beginning and end of the season) should also be protected to ensure population viability. As climate change progresses, increases in sand temperatures and the resultant more strongly biased female sex ratios may necessitate more active management strategies (e.g., shading nests, relocating eggs to hatcheries, re-vegetation) (Fuentes et al., 2012; Jourdan and Fuentes, 2013; Wood et al., 2014). Open air hatcheries could potentially be used in Brazil to ensure that the production of hatchling sex ratios is similar to historical ones (Marcovaldi et al., 2014; Wood et al., 2014). Due to changes in management strategies of TAMAR, the number of relocated nests to open air



**Fig. 5.** Sex ratio as % female (bars) and percentage of loggerhead turtle nests per half month relative to the season's total (line) during all nesting season in A) Sergipe, B) Bahia, C) Espírito Santo and D) Rio de Janeiro.

hatcheries is not as high as they used to be in the past, as a result *in situ* nests now represent 70% of all nest laid. Careful management of open air hatcheries have kept the incubation conditions similar between the hatchery and natural nests, thus the thermal conditions of open air hatcheries generally matches those from *in situ* nests (Baptistotte, 1995; Naro et al., 1999). In the future, the thermal conditions of these hatcheries could be actively manipulated to ensure the production of a specific sex ratio (Marcovaldi et al., 2014; Wood et al., 2014). Nevertheless, careful consideration should be given to the need, effectiveness and risks associated with these strategies (Fuentes et al., 2014; Jourdan and Fuentes, 2013). Ultimately, selection of sex ratio manipulation strategies and their implementation should be guided by the “desired” sex ratio for each location, which in turn must be informed by historical sex ratio production and the operational sex ratio for that population (Jourdan and Fuentes, 2013; Marcovaldi et al., 1997). Given the limited information on risks associated with implementing active strategies, it will be essential for failures and successes to be communicated so that the information acquired can refine management strategies (Fuentes et al., 2014; Fuentes et al., 2012).

Consideration should also be given to the implications of extreme female bias sex ratios to the viability of populations. Little evidence, to date, suggests that a low production of male hatchlings has resulted in low reproductive success within populations (Broderick et al., 2000). Indeed, nesting populations with strong females biased hatchling production have persisted over several decades (Hays et al., 2003). Female biased sex ratios may be compensated by the different breeding patterns of male and female turtles; males have shorter reproductive intervals than females and move between aggregations of receptive females, which will cause operational sex ratios to be more balanced than hatchling sex ratios (Hays et al., 2010; Hays et al., 2014; Stewart and Dutton, 2014). Therefore, the effects of projected feminization of marine turtle on the viability of populations are likely to be less critical than previously suspected (Hays et al., 2010; Hays et al., 2014). Indeed, in the short-term a feminization of marine turtle populations may deliver unexpected conservation benefits by increasing the number of female hatchlings that mature and lay more eggs, eventually increasing the total size of the population and reproductive output (Laloe et al., 2014). This may already be occurring in Brazil, as loggerhead nesting numbers in Bahia (where hatchlings sex ratios are female biased) have increased rapidly since 1998, whereas nesting numbers in Espírito Santo (with hatchling sex ratios closer to parity) have been experiencing a slower rate of growth (Marcovaldi and Chaloupka, 2007). Nevertheless, as the proportion of male hatchlings is reduced from climate change, a possible scenario includes females being unable to find mates leading to reduced fecundity or female infertility, a reduction in effective population size, and loss of genetic variation and under more extreme climate projections, the potential for production of single sex cohorts (Fuller et al., 2013; Mitchell et al., 2010; Wibbels, 2003). Further insights into the full impact of current female bias and potential feminization of marine turtle populations will be obtained by understanding the lower viable limits of the male to female ratio (Lasala et al., 2013). For this, information on the effective population size (total number of individuals that pass on their genes to the next generation) is required (Fuller et al., 2013). Unfortunately these data are not available for the loggerhead population in Brazil, or most other marine turtle populations. To date, anecdotal sightings of mature males exist for foraging areas in the coast of Pernambuco and Rio Grande do Sul, and in coastal areas near nesting beaches in Bahia (TAMAR unpublished data). Thus, an effort should be made to identify mating areas for loggerhead turtles nesting in Brazil, so that further information on male breeding periodicity and gene flow can be obtained. This information together with information on hatchling parentage analysis can provide insights into the operation sex ratio and effective population size of the loggerhead subpopulations nesting in Brazil, which will help elucidate the true implications from predicted global warming. Knowledge of “sex-ratio thresholds” with information of sand temperature

and/or incubation duration and hence sex ratio produced will allow assessments of potential threats at specific nesting areas and potentially trigger active responses. This highlights the need for long-term continuing studies similar to this study that not only provides a sex-ratio baseline in advance of climate change but that also helps identify whether hatchling production is already feminized.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jembe.2016.01.001>.

## Acknowledgement

We thank TAMAR's staff for all the support and numerous other people who assisted in the collection of the incubation duration data over the years. We are also thankful for the help provided by Juliana Andrade with some of the data sorting for this article. MMPBF acknowledges the support of the Special Visiting Scientist Ciências Sem Fronteiras program, and the Earth, Ocean and Atmospheric Science Department at Florida State University. This study adhered to the legal requirements of Brazil, and to all institutional and animal ethics guidelines. Fieldwork in Brazil was carried out by TAMAR (Brazilian Sea Turtle Conservation Program) under the permit # 41987 from SISBIO (Authorization and Information System on Biodiversity), and the Chico Mendes Institute for Biodiversity Conservation (ICMBio)/Ministry of Environment (MMA). The ethics committee from SISBIO and ICMBio considered animal ethics issues related to the project and the experimental design, and specifically approved this study. No animals were sacrificed for this study. [SS]

## References

- Baptistotte, C., 1995. A clarification on the activities f projeto TAMAR, Brazil. *Chelonian Conserv. Biol.* 1, 328–329.
- Baptistotte, C., Scalfoni, J.T., Mrosovsky, N., 1999. Male-producing thermal ecology of a southern loggerhead turtle nesting beach in Brazil: implications for conservation. *Anim. Conserv.* 2, 9–13.
- Broderick, A.C., Godley, B.J., Reece, S., Downie, J.R., 2000. Incubation periods and sex ratios of green turtles: highly female biased hatchling production in the eastern Mediterranean. *Mar. Ecol. Prog. Ser.* 202, 273–281.
- Foley, A.M., Peck, S.A., Harman, G.R., Richardson, L.W., 2000. Loggerhead turtle (*Caretta caretta*) nesting habitat on low-relief mangrove islands in southwest Florida and consequences to hatchling sex ratios. *Herpetologica* 56, 433–445.
- Fuentes, M., Porter, W., 2013. Using a microclimate model to evaluate impacts of climate change on sea turtles. *Ecol. Model.* 251, 150–157.
- Fuentes, M.M.P.B., Hamann, M., Limpus, C.J., 2010. Past, current and future thermal profiles for green turtle nesting grounds: implications from climate change. *J. Exp. Mar. Biol. Ecol.* 383, 56–64.
- Fuentes, M.M.P.B., Fish, M.R., Maynard, J.A., 2012. Management strategies to mitigate the impacts of climate change on sea turtle's terrestrial reproductive phase. *Mitig. Adapt. Strateg. Glob. Chang.* 17, 51–63.
- Fuentes, M.M.P.B., Chambers, L., Chin, A., Dann, P., Dobbs, K., Marsh, H., Poloczanska, E.S., Maisond, K., Turner, M., Pressey, R.L., 2014. Adaptive management of marine megafauna in a changing climate. *Mitig. Adapt. Strateg. Glob. Chang.* 1–16.
- Fuller, W., Godley, B., Hodgson, D., Reece, S., Witt, M., Broderick, A., 2013. Importance of spatio-temporal data for predicting the effects of climate change on marine turtle sex ratios. *Mar. Ecol. Prog. Ser.* 488, 267–274.
- Godfrey, M.H., Mrosovsky, N., 1999. Estimating hatchling sex ratios. In: Eckert, K., Bjorndal, K., Abreu-Grobois, F., Donnelly, M. (Eds.), *Research and Management Techniques for the Conservation of Sea Turtles*. IUCN/SSC Marine Turtle Specialist Group, pp. 136–138.
- Godley, B.J., Broderick, A.C., Downie, J.R., Glen, F., Houghton, J.D., Kirkwood, I., Reece, S., Hays, G.C., 2001a. Thermal conditions in nests of loggerhead turtles: further evidence suggesting female skewed sex ratios of hatchling production in the Mediterranean. *J. Exp. Mar. Biol. Ecol.* 263, 45–63.
- Godley, B.J., Broderick, A.C., Mrosovsky, N., 2001b. Estimating hatchling sex ratios of loggerhead turtles in Cyprus from incubation durations. *Mar. Ecol. Prog. Ser.* 210, 195–201.
- Hamann, M., Fuentes, M.M.P.B., Ban, N., Mocellin, V., 2013. Climate change and marine turtles. In: Wyneken, J., Lohmann, K.L., Musick, J.A. (Eds.), *The Biology of Sea Turtles*. Taylor & Francis Group, Boca Ranton, pp. 353–378.
- Hawkes, L.A., Broderick, A.C., Godfrey, M.H., Godley, B.J., 2007. Investigating the potential impacts of climate change on a marine turtle population. *Glob. Chang. Biol.* 13, 923–932.
- Hawkes, L.A., Broderick, A.C., Godfrey, M.H., Godley, B.J., 2009. Climate change and marine turtles. *Endanger. Species Res.* 7, 137–154.
- Hays, G.C., Broderick, A.C., Glen, F., Godley, B.J., 2003. Climate change and sea turtles: a 150-year reconstruction of incubation temperatures at a major marine turtle rookery. *Glob. Chang. Biol.* 9, 642–646.

- Hays, G.C., Fossette, S., Katselidis, K.A., Schofield, G., Gravenor, M.B., 2010. Breeding periodicity for male sea turtles, operational sex ratios, and implications in the face of climate change Periodicidad Reproductiva de Tortugas Marinas Machos, Proporciones de Sexos Operacionales e Implicaciones Frente al Cambio Climático. *Conser. Biol.* 24, 1636–1643.
- Hays, G.C., Schofield, G., Mazaris, A.D., 2014. Different male versus female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. *Front. Mar. Sci.* 1, Janzen, F.J., 1994. Climate change and temperature-dependent sex determination in reptiles. *Proc. Natl. Acad. Sci.* 91, 7487–7490.
- Jourdan, J., Fuentes, M.M.P.B., 2013. Effectiveness of strategies at reducing sand temperature to mitigate potential impacts from changes in environmental temperature on sea turtle reproductive output. *Mitig. Adapt. Strateg. Glob. Chang.* <http://dx.doi.org/10.1007/s11027-013-9482-y>.
- Iribi, I., Bradai, M.N., 2014. Sex ratio estimations of loggerhead sea turtle hatchlings at Kuriat Islands, Tunisia: can minor nesting sites contribute to compensate globally female-biased sex ratio? *Sci. World J.* 2014, 8.
- Laloe, J., Cozens, J., Renom, B., Taxonera, A., Hays, G.C., 2014. Effects of rising temperature on the viability of an important sea turtle rookery. *Nat. Clim. Chang.* 4, 513–518.
- Lasala, J.A., Harrison, J.S., Williams, K.L., Rostal, D.C., 2013. Strong male-biased operational sex ratio in a breeding population of loggerhead turtles (*Caretta caretta*) inferred by paternal genotype reconstruction analysis. *Ecol. Evol.* 3, 4736–4747.
- Lima, E.P.E., Wanderlinde, J., de Almeida, D.T., Lopez, G., Goldberg, D.W., 2012. Nesting ecology and conservation of the loggerhead sea turtle (*Caretta caretta*) in Rio de Janeiro, Brazil. *Chelonian Conserv. Biol.* 11, 249–254.
- Limpus, C.J., Reed, P., Miller, J.D., 1983. Islands and turtles: the influence of choice of nesting beach on sex ratio. In: Baker, J.T., Carter, R.M., Sammarco, P.W., Stark, K.P. (Eds.), *Proceedings: Inaugural Great Barrier Reef Conference*. JCU Press, Canberra, Australia, pp. 397–402.
- Marcovaldi, M.A., Chaloupka, M., 2007. Conservation status of the loggerhead sea turtle in Brazil: an encouraging outlook. *Endanger. Species Res.* 3, 133–143.
- Marcovaldi, M.A., de Marcovaldi, G.G., 1999. Marine turtles of Brazil: the history and structure of projeto TAMAR-IBAMA. *Biol. Conserv.* 91, 35–41.
- Marcovaldi, M.A., Godfrey, M.H., Mrosovsky, N., 1997. Estimating sex ratios of loggerhead turtles in Brazil from pivotal incubation durations. *Can. J. Zool.* 75, 755–770.
- Marcovaldi, M.A., Lopez, E., Marcovaldi, M.A., Lopez, G.G., Soares, L.S., et al., 2007. Fifteen years of hawksbill sea turtle (*Eretmochelys imbricata*) nesting in Brazil. *Chelonian Conservation and Biology.* 6, 223–228.
- Marcovaldi, M.A.G., Santos, A.J.B., Santos, A.S., Soares, L.S., Lopez, G.G., Godfrey, M.H., López-Mendilaharsu, M., Fuentes, M.M.P.B., 2014. Spatio-temporal variation in the incubation duration and sex ratio of hawksbill hatchlings: implication for future management. *J. Therm. Biol.* 44, 70–77.
- Margaritoulis, D., 2005. Nesting activity and reproductive output of loggerhead sea turtles, *Caretta caretta*, over 19 seasons (1984–2002) at Laganas Bay, Zakynthos, Greece: the largest rookery in the Mediterranean. *Chelonian Conserv. Biol.* 4, 916–929.
- Mitchell, N.J., Janzen, F.J., 2010. Temperature-dependent sex determination and contemporary climate change. *Sex. Dev.* 4, 129–140.
- Mitchell, N.J., Allendorf, F.W., Keall, S.N., Daugherty, C.H., Nelson, N.J., 2010. Demographic effects of temperature-dependent sex determination: will tuatara survive global warming? *Glob. Chang. Biol.* 16, 60–72.
- Mrosovsky, N., Yntema, C.L., 1980. Temperature dependence of sexual differentiation in sea turtles: implications for conservation practices. *Biol. Conserv.* 18, 271–280.
- Naro, M.E., Mrosovsky, N., Marcovaldi, M.A., 1999. Thermal profiles of sea turtle hatcheries and nesting areas at Praia do Forte, Brazil. *Chelonian Conserv. Biol.* 3, 407–413.
- Reis, E.C., Soares, L.S., Vargas, S.M., Santos, F.R., Young, R.J., Bjorndal, K.A., Bolten, A.B., Lobo-Hajdu, G., 2010. Genetic composition, population structure and phylogeography of the loggerhead sea turtle: colonization hypothesis for the Brazilian rookeries. *Conserv. Genet.* 1467–1477.
- Schmid, J.L., Addison, D.S., Donnelly, M.A., Shirley, M.A., Wibbels, T., 2008. The effect of Australian pine (*Casuarina equisetifolia*) removal on loggerhead sea turtle (*Caretta caretta*) incubation temperatures on Keewaydin Island, Florida. *J. Coast. Res.* 214–220.
- Stewart, K.R., Dutton, P.H., 2014. Breeding sex ratios in adult leatherback turtles (*Dermochelys coriacea*) may compensate for female-biased hatching sex ratios. *PLoS One* 9, e88138.
- Wallace, B.P., DiMatteo, A.D., Hurley, B.J., Finkbeiner, E.M., Bolten, A.B., Chaloupka, M.Y., Hutchinson, B.J., Abreu-Grobois, F.A., Amorocho, D., Bjorndal, K.A., Bourjea, J., Bowen, B.W., Dueñas, R.B., Casale, P., Choudhury, B.C., Costa, A., Dutton, P.H., Fallabino, A., Girard, A., Giordot, M., Godfrey, M.H., Hamann, M., López-Mendilaharsu, M., Marcovaldi, M.A., Mortimer, J.A., Musick, J.A., Nel, R., Pilcher, N.J., Seminoff, J.A., Troëng, S., Witherington, B., Mast, R.B., 2010. Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *PLoS One* 5, e15465.
- Wibbels, T., 2003. Critical approaches to sex determination in sea turtles. In: Lutz, P., Musik, J., Wyneken, J. (Eds.), *Biology of Sea Turtles*. CRC Press, pp. 103–134.
- Witt, M.J., Hawkes, L.A., Godfrey, M.H., Godley, B.J., Broderick, A.C., 2010. Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle. *J. Exp. Biol.* 213, 901–911.
- Wood, A., Booth, D.T., Limpus, C.J., 2014. Sun exposure, nest temperature and loggerhead turtle hatchlings: implications for beach shading management strategies at sea turtle rookeries. *J. Exp. Mar. Biol. Ecol.* 451, 105–114.
- Zbinden, J.A., Davey, C., Margaritoulis, D., Arlettaz, R., 2007. Large spatial variation and female bias in the estimated sex ratio of loggerhead sea turtle hatchlings of a Mediterranean rookery. *Endanger. Species Res.* 3, 305–312.