

**Factors affecting the reproductive output and hatching success of the leatherback sea turtle *Dermochelys coriacea* in Tobago, West Indies<sup>1</sup>.**

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## Abstract

Leatherback populations have experienced significant population declines and are at serious risk of global extinction. Overall offspring survival is vital for the recovery of declining populations and the aim of this study was to examine the factors that may influence clutch size and hatching success of the nesting leatherback population in Tobago. The study analysed nesting and hatching data collected from three beaches (Turtle Beach, Grafton, Back Bay) during the 2009-2012 nesting seasons. High inter-individual variation was found in curved carapace length and clutch size, but there was no association between the two variables. On the other hand, clutch size decreased as season progressed. Mean hatching success was  $58 \pm 26\%$ , similar to the reported rates for leatherbacks worldwide. Success of clutches laid towards the end of the season decreased. This could be due to many factors including: climatological factors or/and reduced fertility in turtles that arrive later in the nesting season. Differences in hatching success among beaches and zones seemed to be related to the amount of human activity and coastal hazards. In addition, hatching success decreased significantly in clutches that had signs of bacterial infestation. This study has shown that variation in reproductive output could not be explained by body size and that hatching success was affected by the day within season the clutch was laid, the location and the presence of bacteria in the clutch. Further research is required to develop a more complete understanding of the potential role of pathogenic bacteria and the consequences of differential resource availability on reproductive output and hatching success. Recovery of sea turtle populations requires a holistic approach that includes effective beach and marine ecosystem conservation.

## 1. Introduction

The leatherback sea turtle *Dermochelys coriacea* is the largest of the seven living species of sea turtles (Bell et al., 2003) and the only extant species within the family Dermochelyidae (Rafferty et al., 2011). It is one of the most widely distributed reptiles that nests on oceanic beaches in tropical and sub-tropical regions worldwide (Reina et al., 2002; Bell et al., 2003; Spanier, 2010; Conrad et al., 2011). It was once thought to be the most abundant sea turtle species in the world but has suffered substantial population declines (Pritchard, 1982; Spanier, 2010; Rafferty et al., 2011). Despite continuing conservation efforts, it has been estimated that the global population of leatherbacks has been reduced by 67% (Rafferty et al., 2011). It is considered to be at a serious risk of global extinction (Dutton et al., 2005), and is classified as critically endangered by the Species Survival Commission (IUCN) (Hilton-Taylor, 2000).

The decline in the numbers of leatherbacks has been mainly attributed to anthropogenic causes such as offshore fishing, egg poaching and habitat degradation (Spotila et al., 1996, 2000; Sarti-Martínez, 2000). However, natural processes such as low

hatching success and the loss of eggs due to beach erosion and bacterial infestation are considered to be important factors that reduce overall offspring survival (Bell et al., 2003; Spanier, 2010; Rafferty et al., 2011) which is an important component for growth and recovery of declining populations (Dutton et al., 2005). Leatherbacks have an average hatching success of 50% worldwide, lower than all other sea turtle species, which have an average success of over 80% (Miller, 1997; Rafferty et al., 2011). Low hatching success in leatherbacks has been attributed to high levels of embryonic death (Bell et al., 2003). Several studies have been conducted to determine links between embryonic death and environmental factors (Wallace et al., 2004; Ralph et al., 2005; Caut et al., 2006; Santidrián-Tomillo et al., 2009; Garrett et al., 2010), but the results are highly variable suggesting the need for further research. Moreover, it has been hypothesised that biological factors, such as clutch size (Hewavishenthi and Parmenter, 2002; Garrett et al., 2010) and number of shelled albumen gobs (SAGs; packets of excess albumen formed in the oviduct and covered with a shell, Bell et al., 2003) laid per clutch may also affect the hatching success of viable eggs (Whitmore and Dutton, 1985; Caut et al., 2006).

One of the factors that affect the reproductive output of sea turtles is the number of eggs that are laid per clutch (Santidrián-Tomillo et al., 2009). Among populations variations in morphology may contribute to reproductive output variations (Broderick et al., 2003). Nesting is a process that results in high-energy expenditure, therefore, sea turtles are expected to maximise clutch size and increase clutch size with body size (Hays & Speakman, 1991). It has been suggested that larger turtles may be physically capable of carrying more eggs compared to smaller turtles (Hays & Speaksman, 1991; Price et al., 2004). Indeed, several studies have revealed a positive correlation between adult body and clutch size in many sea turtle species (Pinckney, 1990; Hays and Speaksman, 1991; Broderick et al., 2003) including leatherbacks (Hirth and Ogren, 1987; Van Buskirk and Crowder, 1994; Price et al., 2004). However, in a few other studies variation in clutch size could not be explained by female body size (Bjorndal and Carr, 1989; Tucker and Frazer, 1991; Reina et al., 2002; Wallace et al., 2007).

In the Wider Caribbean Region sea turtle populations have been severely reduced from their historical levels and are considered to be “virtually extinct” in terms of their role in Caribbean marine ecosystems (Bjorndal and Jackson, 2003; Dow-Piniak and Eckert, 2011). The Republic of Trinidad and Tobago supports the second largest nesting assemblage of leatherbacks in the Western Hemisphere (Fournillier and Eckert, 1998; Eckert, 2001; Turtle Expert Working Group, 2007). Beaches with high nesting activity are found on the north and east coasts of Trinidad and on the southwest coast of Tobago (Fig. 1) (Bacon, 1970; Chu Cheong, 1990). The leatherback nesting colony on the southwest cost of Tobago has been the subject of a long-term monitoring program since 2000 conducted by Save Our Sea Turtles

(SOS) Tobago, which is a registered community based organization and a member of the Wider Caribbean Sea Turtle Conservation Network (WIDECAST).

The aim of this study was to investigate the factors that may have an effect on the size and hatching rates of leatherback clutches in Tobago. Obtaining this kind of information is important for conservation purposes as it provides a baseline for exploring the ability of turtles to adapt to changes in the environment due to the on going global climate change. More specifically, the objectives were (a) to examine the variation in reproductive output among the population by investigating whether there was a relationship between female body size and clutch size, and how the variation in clutch size changed over time throughout a nesting season; (b) to examine hatching success by investigating if and how it was affected by clutch size, number of SAGs, depth of egg chamber, bacterial infestation, incubation time, location, time of season and nesting year; and (c) to examine if bacterial infestation of clutches was associated with individual nesting females, location, and nesting time within the season the clutches were laid.

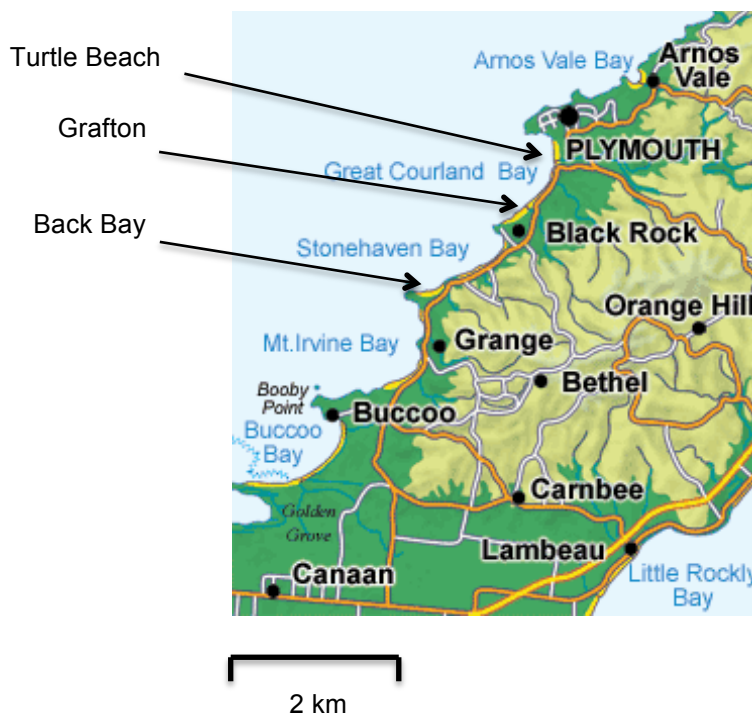
## **2. Methods**

### *2.1 Ethics statement*

This study was approved by the Department of Natural Resources and the Environment of Tobago, the permitting and regulatory authority in Tobago.

### *2.2 Study site and data collection*

The study was conducted in Tobago in collaboration with Save Our Sea Turtles (SOS) Tobago. Tobago is located in the West Indies at the southernmost point of the Caribbean archipelago (11°9' N, 60°40' W). The coastline presents a range of anthropogenic influence from urban to near wilderness state. Data were collected from three main nesting beaches on the southwest coast (Fig. 1) comprising a coastline of 2.6 km in length, Turtle Beach (1.2 km), Grafton (0.9 km) and Back Bay (0.5 km) during the nesting seasons 2009-2012 (March-October). The beaches were divided into zones; Turtle Beach Zones 1-2-3-4, Grafton Beach Zones 1-2-3, and Back Bay Zones 1-2. All zones were patrolled nightly on foot between 8pm to 4am at 30min intervals to ensure that all nesting females were encountered.



**Fig. 1. Map of Tobago showing the location of the study sites, Turtle Beach (TB), Grafton (GR) and Back Bay (BB).**

Every nesting turtle encountered was approached at the time of oviposition, during which they are nonresponsive to manipulation (Dutton and Dutton, 1994), to minimise disturbance and the risk of nest abandonment. The flap of skin between the tail and the rear flipper, on each side, was tagged with a metal numbered tag (#1005-49R MONEL Tag), or if already tagged, the tag numbers were noted. In addition, curved carapace length (CCL) and

curved carapace width (CCW) were measured with a flexible measuring tape to the nearest cm. CCL was the distance from the centre of the nuchal notch along the side of the dorsal ridge to the posterior tip of the carapace (pygal process). CCW was the distance across the carapace from the widest point along the most lateral ridge (4th longitudinal) to the widest point on the opposite lateral ridge (Steyermark et al., 1996). Multiple measurements within a season were averaged to determine a turtle's size, assuming that no detectable growth occurred during the breeding season (Broderick et al., 2003). Latitude and longitude coordinates of the nest sites, accurate to within 3 m, were recorded by a global positioning system (GPS; model Garmin eTrex H).

Nests were excavated after the first observance of signs of hatchling emergence to estimate hatching success. Not all nests were excavated because some were lost due to beach erosion, inundation, or could not be located as no hatchling tracks were observed. From the nests that were excavated the contents were removed and the depth of the egg chamber was measured with a flexible measuring tape to the nearest cm, from the bottom to the beach surface. All hatched, pipped (not hatched egg; hatchling has broken through the egg shell but is not completely free of shell) and unhatched eggs were counted together with SAGs. The clutch size was estimated by adding hatched, pipped and unhatched eggs together and subtracting the SAGs (Van Buskirk and Crowder, 1994). Unhatched eggs were opened and their content was recorded. Bacterial infestation of eggs was determined by direct observation. Eggshells accounting to more than 50% of an egg were recorded as one egg (Miller, 1999). When eggshells were fragmented pieces were grouped together to represent one egg (Caut et al., 2006b, Caut et al., 2010). The percent hatching success was estimated using the following formula:  $\text{hatched shells}/\text{total yolked eggs laid} \times 100$  (Eckert and Eckert, 1990). The incubation period was calculated as the number of days from oviposition until the first hatchlings reached the beach surface (Van Buskirk and Crowder, 1994). Day 1 of the nesting season was determined as the day that the first clutch was laid among the ones that had hatched and had been excavated.

### *2.3 Statistical analyses*

The dataset from the 2012 nesting season was used for the examination of the effect of variables on reproductive output and hatching success. It was the only nesting season during which information of the nesting female turtle (CCL, CCW and tag numbers) was recorded for the nests and made it possible to associate the excavated nests to specific individuals. The datasets from all the seasons (2009-2012) were used to examine differences in hatching success among nesting seasons. Initially, descriptive statistics were performed to summarise the variables taken into consideration. Prior to analysis, variables were screened for normality using the Shapiro-Wilk test, histograms and quantile-quantile plots. Correlations were used to examine the relationships between explanatory variables. The Pearson correlation coefficient

was used for parametric variables and the Spearman correlation coefficient for non-parametric variables. The correlation coefficients were used to decide whether variables were collinear and able to be used together in the multivariate models. Statistical significance was accepted at the 0.05 level and all means are reported as  $x \pm SD$  (standard deviation). All data analyses were conducted with the software R (R 3.0.1, R Development Core Team, 2013).

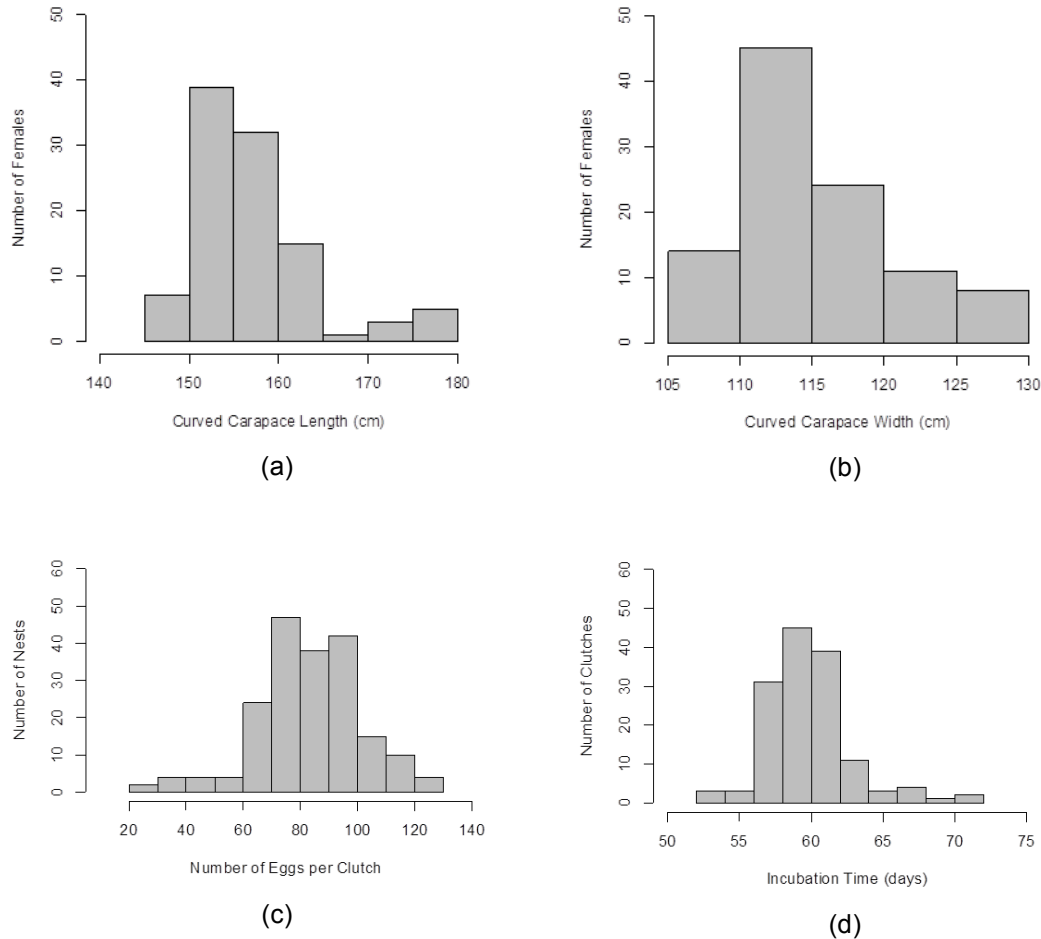
Univariable generalised linear regression with a poisson distribution was used to examine the effect of CCL and day of season on clutch size (count data). Univariable generalised linear models were used to examine the impact of various variables upon hatching success. The predictors were clutch size, egg chamber depth, incubation time, day of nesting season, location, proportion of SAGs, and the presence of bacterial infestation in the clutch. The predictors were then included in a multivariable model to find a combination of factors that best explained hatching success. Backwards stepwise elimination was used to remove the least significant covariates until the model was no longer improved from additional removal of covariates (Chouinard and Arnold, 2007; Platts et al., 2008). The significant covariates were determined by p-value and the models were compared using the Akaike Information Criterion (AIC) (Burnham and Anderson, 2004; Burnham et al., 2011). *Post hoc* analysis was used to investigate whether there were any significant differences in mean hatching success among the three beaches, and then more specifically among the 4 zones of Turtle Beach that had a significantly lower hatching success compared to Grafton and Back Bay. The data from all seasons (2009-2012) were used in order to examine the effect of year on hatching success using binomial regression. Because there was a significant effect of year on the hatching success, *post hoc* analysis was performed to examine differences among nesting seasons. Finally, logistic regression was used to investigate whether the identity of the nesting female, the day within the season that the nest was laid and the location of the nest (Turtle Beach, Grafton, Back Bay) had an impact on the bacterial infestation of the clutches. Bacterial infestation was a dichotomous dependent variable coded as 1 – presence of bacteria within the clutch and 0 - absence of bacteria within the clutch.

### **3. Results**

#### *3.1 Descriptive analyses of the basic parameters*

Throughout the 2012 nesting season a total of 102 individual nesting female leatherback turtles were measured and 194 nests were excavated. Mean CCL was  $157.3 \pm 6.9$  cm (Fig. 2(a)). Mean CCW was  $115.6 \pm 5.8$  cm (Fig. 2(b)). The number of yolked eggs laid by each nesting female ranged from 20-127 ( $84 \pm 18$  eggs) (Fig. 2(c)). The number of SAGs ranged from 0-63 ( $26 \pm 13$ ). The proportion of SAGs per clutch ranged from 0-66% ( $24 \pm 11\%$ ). 93% of the clutches had signs of bacterial infestation. The proportion of eggs with bacteria per clutch ranged from 0-93% ( $23 \pm 19\%$ ). Mean hatching success was  $58 \pm 26\%$

(range = 0-100%). The mean depth of the egg chamber was  $78.7 \pm 8.4$  cm with a range of 52-108 cm ( $n = 187$ ). The mean incubation period of clutches was calculated at  $60 \pm 3$  days ( $n = 142$ ) (Fig. 2(d)).



**Fig. 2. Frequency distributions of the curved carapace length (cm) (a), curved carapace width (cm) (b) of nesting females, and clutch size (c) and days of incubation (d) of clutches laid in 2012 nesting season.**

### 3.2 Effects on clutch size

Clutch size was not significantly affected by CCL (Table 1) indicating that variation in reproductive output among females cannot be explained by body size. On the other hand, at a population level, the day within nesting season had a significant effect on clutch size (Table 1). The number of yolked eggs laid by each nesting female was slightly decreased as the nesting season progressed.



**Table 1**

**Univariable Poisson Generalised Linear Model (GLM) analysis of curved carapace length (cm) of nesting females and day within season the clutch was laid on the number of yolked eggs per clutch laid in 2012 nesting season.**

<b>Clutch Size</b>	<b>Estimate</b>	<b>Standard Error (SE)</b>	<b>z value</b>	<b>P value</b>
<b>CCL</b>	0.001	0.002	0.709	0.478
<b>Nesting Day</b>	-0.001	0.000	-2.381	0.017

### 3.3 Effects on hatching success

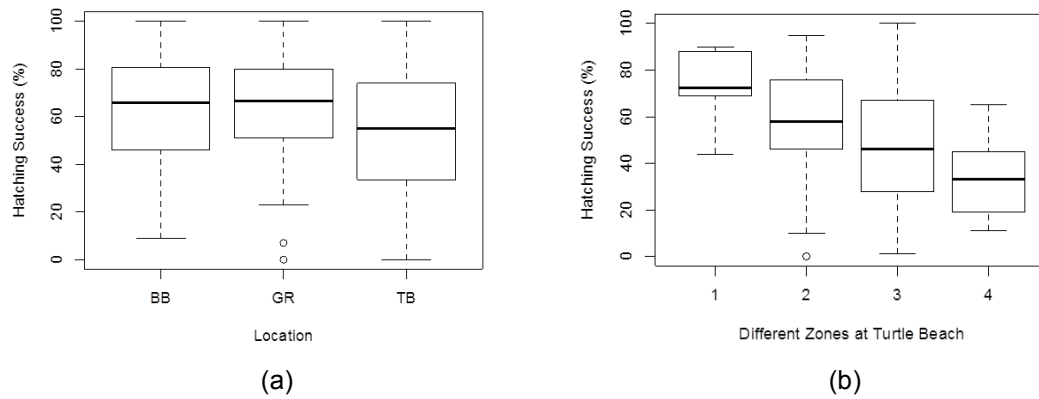
Hatching success was not significantly affected by the depth of the egg chamber, the size of the clutch, the percentage of SAGs per clutch and the incubation time (Table 2). The day within season the clutch was laid and the presence of bacteria in the clutch had a significant negative effect on hatching success. Hatching success was slightly decreased as the nesting season progressed and greatly decreased with the presence of bacterial infestation in the clutch (Table 2). Location had a significant effect on hatching success with one beach being associated with a lower level of hatchling success than the others (Table 2). A better model was not obtained when all the predictors were included in a multivariable model to find a combination of factors that best explain hatching success.

**Table 2**

**Univariable GLM analysis of all predictors on hatching success (%) of clutches laid in 2012 nesting season.**

<b>Hatching Success</b>	<b>Estimate</b>	<b>SE</b>	<b>t value</b>	<b>P value</b>
<b>Nest Depth</b>	0.052	0.222	0.233	0.816
<b>Clutch Size</b>	-0.090	0.101	-0.886	0.377
<b>SAGs</b>	0.269	0.159	1.693	0.092
<b>Incubation Time</b>	-1.014	0.698	-1.453	0.149
<b>Bacteria</b>	-18.490	7.217	-2.562	0.011
<b>Nesting Day</b>	-0.146	0.058	-2.498	0.014
<b>Location GR</b>	1.432	5.318	0.269	0.788
<b>Location TB</b>	-8.905	4.392	-2.028	0.044

Due to a significant effect of location on hatching success, differences among locations were examined with *post hoc* analysis. The mean hatching success was  $63 \pm 25\%$  at Back Bay ( $n = 48$ ),  $64 \pm 22\%$  at Grafton ( $n = 42$ ) and  $54 \pm 27\%$  at Turtle Beach ( $n = 104$ ) (Fig. 3(a)). Turtle Beach had the lowest hatching success and a *post hoc* analysis showed that there was a significant difference among Zones 1-2-3-4. More specifically, mean hatching success was  $74 \pm 15\%$  at Zone 1 ( $n = 14$ ),  $57 \pm 25\%$  at Zone 2 ( $n = 32$ ),  $49 \pm 28\%$  at Zone 3 ( $n = 49$ ) and  $34 \pm 19\%$  at Zone 4 ( $n = 9$ ) (Fig. 3(b)).



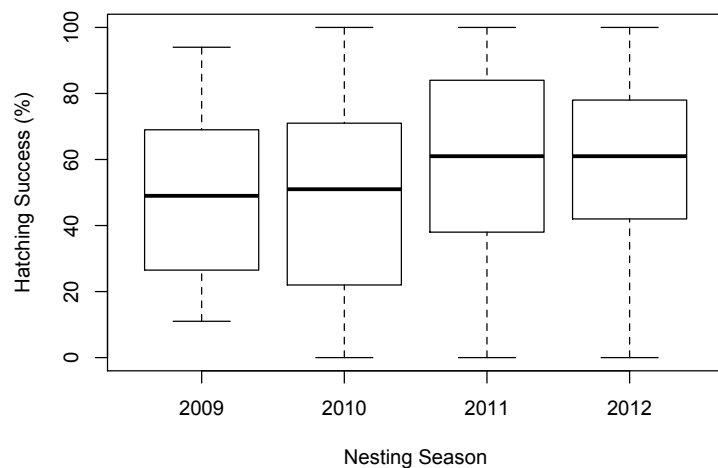
**Fig. 3. Hatching success (%) of clutches laid at Back Bay (BB), Grafton (GR) and Turtle Beach (TB) (a), and Zones 1-2-3-4 at Turtle Beach (TB) (b) in 2012 nesting season.**

The effect of nesting season on hatching success was examined taking into consideration the data from years 2009-2012. Nesting season had a significant effect on hatching success (Table 3) and *post hoc* analysis showed that there was a significant difference in hatching success between nesting seasons 2010 and 2011, and between nesting seasons 2010 and 2012. The mean hatching success was  $48 \pm 26\%$  in 2009 ( $n = 27$ ),  $48 \pm 27\%$  in 2010 ( $n = 126$ ),  $60 \pm 27\%$  in 2011 ( $n = 168$ ) and  $58 \pm 26\%$  in 2012 ( $n = 194$ ) (Fig. 4).

**Table 3**

**Univariable GLM analysis of nesting season on hatching success (%).**

Hatching Success	Estimate	SE	t value	P value
<b>2010</b>	-0.225	5.568	-0.040	0.968
<b>2011</b>	11.537	5.444	2.119	0.035
<b>2012</b>	10.094	5.393	1.872	0.062



**Fig. 4. Hatching success (%) of clutches laid in 2009, 2010, 2011 and 2012 nesting seasons.**

### *3.4 Effects on bacterial infestation*

Maternal identity, location of nest, and day of nesting season that the clutch was laid had no significant effect on the presence or absence of bacterial infestation of clutches laid in 2012 nesting season.

## **4. Discussion**

### *4.1 Effect on clutch size*

Female leatherback turtles nesting in Tobago exhibited high inter-individual variation in body size measured by CCL (Fig. 2(a)) and in the number of yolked eggs laid per clutch (Fig. 2(c)). Despite numerous reports and wide support for the relationship between female size and clutch size in many sea turtle species (Pinckney, 1990; Hays and Speaksman, 1991; Broderick et al., 2003) including leatherbacks (Hirth and Ogren, 1987; Van Buskirk and Crowder, 1994; Price et al., 2004), female body size accounted for little to none of the variation in size of the clutches laid in Tobago (Table 1). The current finding is in accordance with previous findings from several studies on leatherback turtles (Bjorndal and Carr, 1989; Tucker and Frazer, 1991; Reina et al., 2002; Wallace et al., 2007). This indicates that physical constraints such as available body cavity space do not appear to influence patterns of maternal investment in reproduction in this population of leatherbacks.

At a population level, as the season progressed clutch size slightly decreased (Table 1). This finding contradicts reproductive optimality models predicting that species that lay several, large clutches per reproductive season, such as sea turtles, should exhibit low variation in egg size and instead maximise clutch size and frequency (Smith and Fretwell, 1974; Congdon and Gibbons, 1987; Hays and Speakman, 1991). Leatherbacks lay the highest number of clutches, from four to eight per nesting season, compared to other sea turtle species (Miller, 1997; Fretey and Girondot, 1998; Eckert, 2001). They increase their seasonal reproductive output by increasing the number and size of their clutches (Wallace et al., 2007) to compensate for high and unpredictable mortality during early life stages (Mrosovsky, 1983). However, a decrease in clutch size as season progresses has also been reported in loggerheads (Broderick et al., 2003).

### *4.2 Effect on hatching success*

Mean hatching success of clutches laid throughout 2012 nesting season was similar to the reported lower average hatching rates for leatherbacks when compared to other sea turtle species (Miller, 1997; Rafferty et al., 2011). High embryonic mortality has been suggested as

the main reason of low hatching rates (Bell et al., 2003) implicating physical and biological factors that affect embryonic development (Garrett et al., 2010). Among sea turtle species leatherbacks lay their eggs in the deepest nests of around 70-100cm (Wallace et al., 2007). Increasing depth of the egg chamber may result in increasing water content and salinity of the sand that could lead to a decrease in hatching success (Foley, 2006). Nonetheless, variation in nest depth had no significant effect on hatching success (Table 2). However, the findings of previous studies have not been consistent. Similar results have been reported by Ozdemir and Turkozan (2006) and Martins et al. (2008) for green and loggerhead turtles. On the other hand, Mortimer (1990) found that clutch survival was positively correlated with nest depth in green turtles, while Hall (1990) reported a slight negative correlation in leatherbacks.

Variation in clutch size has also been investigated in terms of its effect on hatching success and it has been suggested that the benefits of an increased clutch size may be due to better gas exchange, reduced air cavities or improved temperature regulation (Ackerman, 1981; Mortimer, 1990; Ditmer and Stapleton, 2012). In leatherbacks in Tobago clutch size had no significant effect on hatching success (Table 2). Likewise, no significant relationship was reported in green turtles (Mortimer, 1990). On the other hand, a significant positive relationship was found in flatback (Hewavisenthi and Parmenter, 2002) and hawksbill turtles (Ditmer and Stapleton, 2012). On average, leatherback clutches contain 21-56 SAGs (Leslie et al., 1996, Maros et al., 2003). Hatching success was not affected at a significant level by the proportion of SAGs per clutch in Tobago (Table 2). However, other studies have reported a positive relationship between clutch survival and number of SAGs (Hall, 1990; Caut et al., 2006). It has been proposed that they may provide some selective advantage and improve the hatching success of the viable eggs (Whitmore and Dutton, 1985) by maintaining physicochemical conditions in the nest (Dutton and McDonald, 1995) or by acting as decoys for predators (Caut et al., 2006). Incubation time was not found to affect the hatching success of leatherback clutches in Tobago (Table 2). However, shorter incubation times have been shown to result in higher hatching success in loggerhead turtles (Pinckney, 1990). On the other hand, a significant temporal effect on hatching success was found. Hatching rates decreased with nesting season progression (Table 2). This finding is in accordance with the findings of previous studies on leatherbacks (Santidrián-Tomillo et al., 2009; Rafferty et al., 2011).

The presence of bacteria had a significant effect on the hatching success of clutches. Hatching success decreased greatly in clutches that had signs of bacterial infestation (Table 2). Although not all bacteria that can infect sea turtle eggs are necessarily pathogenic (Soslau et al., 2011), there have been several studies that have identified bacteria associated with unhatched turtle eggs of leatherbacks (Girondot et al., 1990; Zieger et al., 2009; Soslau et al., 2011), loggerheads (Wyneken et al., 1988; Awong-Taylor et al., 2008; Craven et al., 2007) and olive ridleys (Mo et al., 1990). Sea turtle eggs are deposited into moist sand and are

exposed to a host of bacteria that can infect the developing embryo by penetrating the eggshell through the pores and contaminating both albumen and yolk (Al-Bahry et al., 2009). In addition, bacteria may be transferred to the eggs from the female's cloaca fluid during oviposition (Zieger et al., 2009; Soslau et al., 2011). Further analysis was conducted to investigate whether the presence of bacteria in the clutch could be explained by the identity of the nesting female, the beach and the time within the season that the clutch was laid. However, no association was found.

Nest location significantly affected the hatching success of leatherback clutches (Table 2). Clutches located at Turtle Beach had a much lower success compared to those located at Back Bay and Grafton. In addition, hatching success was significantly variable among the 4 zones at Turtle Beach (Fig. 3(b)). Leatherbacks tend to nest on dynamic oceanic beaches that erode and accrete seasonally (Eckert, 1987; Conrad et al., 2011) and it has been estimated that 36-50% of nest loss is due to beach erosion and inundation (Mrosovsky, 1983; Patino-Martinez et al., 2008). All three beaches are highly dynamic and unstable and can be greatly affected by high tides and storms. Back Bay is a relatively undisturbed beach, while Grafton and Turtle Beach are more heavily used by people. Turtle Beach has the highest human related activity compared to the other two. More specifically, zone 2 is the most developed and heavily used part of the beach and zone 3 is frequently used for large public events that are held during the nesting season. On the other hand, zones 1 and 4 are the areas least used by humans. However, the ends of both zones are crossed by rivers that may occasionally open, especially after heavy rains, and overwash incubating nests. Therefore, differences in hatching success among beaches and zones could be possibly explained by the amount of human activity on the beach that could cause sand compaction (Patino-Martinez et al., 2008) and by coastal hazards, such as flooding events and beach erosion (Caut et al., 2010). Finally, there were significant differences in hatching success among nesting seasons (Table 3, Fig. 4).

#### *4.3 Limitations of the study*

In this study reproductive output was examined measured by clutch size. Considering the high number of clutches that leatherbacks lay per nesting season clutch frequency would also be necessary to be accounted for assessing changes in seasonal fecundity. However, throughout the nesting season only a small number of nesting females were reported to have returned several times to nest at the study sites. Consequently, not enough data were available to investigate this parameter. Moreover, it has been suggested that other features of body size such as body volume and mass may have a greater effect on the clutch size of leatherbacks (Broderick et al., 2003; Wallace et al., 2007). However, minimum disturbance is a priority in the conservation of sea turtles, therefore weighing individual females would not be justified (Broderick et al., 2003). In terms of hatching success, abiotic factors in the nest such

as temperature and humidity may affect the development of sea turtles during incubation (Davenport, 1997). Moreover, rainfall (Houghton et al., 2007) and tidal inundation (Eckert, 1987) may influence success rates. However, no data were available to investigate the impact of these factors. With regards to bacterial infestation, the presence of bacteria was determined by direct observation without taking samples and isolating them. Therefore, their presence could not be accurately concluded. Finally, the results should be interpreted cautiously taking into consideration the heterogeneity of the data-collection efforts and the variable experience of the surveyors.

#### *4.4 Implications of the study*

The contradicting results between studies on the relationship of body size and clutch size may indicate that CCL is not a good indicator of the female's egg carrying capacity (Hays and Speakman, 1991). Moreover, they may reflect that factors other than CCL account for the variation in clutch size. It has been suggested that environmental stochasticity, specifically differential resource availability accounts for differences in body size and reproductive output between different populations (Olsson and Shine, 1997; Jordan and Snell, 2002; Wallace et al., 2006). Therefore, it could be speculated that dietary variations may have an impact on reproductive output of nesting females in Tobago. Moreover, it has been proposed that variation in clutch size may be also associated with resource availability (Broderick et al., 2003). Therefore dietary factors such as depletion of resources may account for the within-season decrease in the number of eggs laid per clutch. Leatherbacks feed primarily on pelagic gelatinous zooplankton (Bjorndal, 1997) and spend much of their time searching for prey patches (Hays et al., 2006; Doyle et al., 2008). However, they appear to be greatly resource-limited in their foraging habitats (Wallace et al., 2006). A study on habitat use by leatherbacks in the North Atlantic has revealed that shifts in the location of the 15°C isotherm can affect greatly the available foraging habitat (McMahon and Hays, 2006). Therefore, climatic factors that affect in direct or indirect ways the thermal environment and resource availability may strongly affect the acquisition of energy by turtles, which in turn could be detectable in their reproductive periodicity and output (Reina et al., 2009).

In terms of hatching success, the decreased success rates of clutches laid toward the end of the season could be explained by climatological factors such as increases in temperature (Rafferty et al., 2011) or/and by reduced fertility in turtles that arrive later in the nesting season (Bell et al., 2003). Furthermore, location was demonstrated to have a great impact, and the differences in success rates between different beaches and zones seem to be related to human activity and coastal hazards. Also, considering the tendency of leatherbacks to nest close to the high-tide line (Whitmore and Dutton, 1985; Kamel and Mrosovsky, 2004) it should be noted that anthropogenic global warming poses a serious threat for the viability of their nests (Caut et al., 2010). It has been predicted that sea level will

rise 0.6m during the next century (IPCC, 2007) and the consequences of this rise are likely to include more frequent flooding events and exacerbated beach erosion (Fish et al., 2008; Caut et al., 2010) that may result to a decrease in hatching success in the future due to overwash of nests. In addition, although causes of egg failure and embryonic death of sea turtles are not always clear, it has been suggested that bacterial contamination may have a potential role (Wyneken et al., 1988). Isolated species from turtle clutches have been associated with diseases in a variety of chelonians (Zieger et al., 2009). Infections by pathogenic bacteria may explain significant losses of developing embryos as it has been described in loggerhead eggs (Wyneken et al., 1988).

## **5. Conclusion and further research**

This study provides insights as to how various factors may influence the reproductive output and hatching success of leatherbacks and sea turtles in general. Variation in reproductive output could not be explained by body size and hatching success was affected by the day within season the clutch was laid, the location and the presence of bacteria in the clutch. Clutch size slightly decreased as the nesting season progressed, but this does not necessarily imply a decrease in fecundity. Depletion in resources needs to be investigated further in terms of its association with the variation in clutch size within the nesting season. In terms of hatching success, anthropogenic factors such as human related activity on the beaches seem to have a negative impact on the success rates. Additional research is needed to investigate potential changes in fertility as the nesting season progresses. Also, isolation and identification of the number and species of bacteria present in clutches is required to develop a more complete understanding of their potentially pathogenic role in hatching success. Finally, depletion of resources and climate change need to be investigated further in terms of the reproductive output and hatching success of sea turtles. Climate change could possibly affect the reproductive output of sea turtles through altered foraging conditions, and also increase the risk of nest losses in beaches susceptible to coastal hazards. To conclude, conservation of sea turtle populations requires a holistic approach that includes, among other efforts, effective beach conservation to protect nesting females and their eggs and maximise overall hatchling production, as well as effective conservation and sustainable use of marine ecosystems to protect their foraging habitats.

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