



Effects of egg mass and local climate on morphology of East Pacific leatherback turtle *Dermochelys coriacea* hatchlings in Costa Rica

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ABSTRACT: Global climate patterns are shifting due to anthropogenic causes, putting pressure on many species that are unable to adapt to such rapid changes. Sea turtle clutches, for example, normally develop between 26 and 33°C, but tolerate higher temperatures at the end of development. High temperatures, protracted rainfall, and droughts have been linked to fewer hatchlings. Likewise, climatic conditions can affect the size of sea turtle hatchlings, which could affect their probability of survival. We analyzed the effects of a biotic factor (egg mass) and environmental factors (precipitation and incubation temperature) on East Pacific leatherback turtle *Dermochelys coriacea* hatchling sizes in Costa Rica. Hatchling size (mass, straight carapace length, straight carapace width, and head width) was affected by both biotic and environmental factors. While egg mass was the strongest predictor for hatchling mass, temperature was the strongest for carapace length and head width. Carapace width was most strongly predicted by precipitation. Hatchling carapace length and width decreased with increases in temperature and increased with higher levels of precipitation. Hatchling mass also decreased with increasing temperature, although the relationship was not statistically significant. Head width decreased with greater precipitation during development. These findings suggest that increases in temperature and decreases in precipitation may not only decrease the number of hatchlings produced, but may also produce smaller leatherback hatchlings in Pacific Costa Rica, which may impair hatchling survival in the first hours after emergence.

KEY WORDS: Climate change · Hatchling size · Sea turtle · Egg mass · Temperature

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1. INTRODUCTION

Rising global air temperatures and changes in precipitation patterns due to anthropogenic causes are affecting climate worldwide (Karmalkar et al. 2011, Intergovernmental Panel on Climate Change in press). Depending on their life histories, some species may respond to climate change either by modifying their behavior or by shifting their ranges (Davis &

Shaw 2001, Chen et al. 2011, Milazzo et al. 2013, Beever et al. 2017). However, these strategies are not realistic for some species that are not mobile for all or part of their lifespans, do not exhibit behavioral plasticity, or whose ranges are restricted (Davis & Shaw 2001, Burrows et al. 2014, Beever et al. 2017). These species are especially vulnerable to shifts in climate because they are unable to escape detrimental temperatures (Beever et al. 2017).

Sea turtles, for example, are highly mobile as adults (Hays et al. 2004, Benson et al. 2007, Shillinger et al. 2008), but return to the same general area where they hatched to lay their clutches, and their eggs are completely dependent on their immediate environment (Benson et al. 2007, Santidrián Tomillo et al. 2012, 2014). Many nesting sites have begun to experience warming trends, and temperatures are predicted to continue to rise (Hays et al. 2003, Saba et al. 2012, Fuentes & Porter 2013, Santidrián Tomillo et al. 2015a). This presents a possible issue for sea turtle nests because during development, eggs are immobile and dependent on the environmental conditions inside the nest to provide suitable temperature and humidity, both of which are affected by local climatic conditions (Ackerman 1997, Hays et al. 2003, Dore 2005, Santidrián Tomillo et al. 2012, 2014, Fuentes & Porter 2013).

Temperature within the nest determines the sex of sea turtle offspring, a mechanism shared by many reptiles called temperature-dependent sex determination (Morreale et al. 1982, Janzen & Paukstis 1991, Binckley et al. 1998). In sea turtles, high temperatures during the middle third of embryonic development produce female hatchlings and low temperatures produce males (Morreale et al. 1982, Pieau & Mrosovsky 1991). Therefore, increases in nest temperature can also increase production of female offspring, although this may be limited by the effect of high temperature on egg and hatchling mortalities (Santidrián Tomillo et al. 2014).

Temperature and precipitation can affect the rate of embryonic development as well as the quantity of eggs that successfully hatch. For example, protracted precipitation can greatly reduce nest temperatures (Houghton et al. 2007), and local climatic conditions that are too dry or too wet for embryonic development can reduce hatching and emergence success of nests (Patino-Martinez et al. 2014, Santidrián Tomillo et al. 2015b). Precipitation can additionally affect nesting beach dynamics, including flooding and erosion that could be fatal to sea turtle nests (Dewald & Pike 2014, Rivas et al. 2018, Limpus et al. 2021).

Both higher incubation temperatures and extremely high and low nest humidity have also been linked to smaller hatchlings (McGehee 1990, Glen et al. 2003, Read et al. 2013) and poor locomotor performance in hatchlings of sea turtles and various other reptile species (Booth 2006, Patino-Martinez et al. 2014, Kobayashi et al. 2017, Gatto & Reina 2020). Because hatchlings experience the greatest risk from predators while navigating the beach and nearshore waters (Gyuris 1994, 2000, Pilcher et al. 2000, San-

tidrián Tomillo et al. 2010), those that reach the open ocean quickest may have the best chance of survival (Booth et al. 2004, Mickelson & Downie 2010, Hart 2016). Some studies have suggested that larger hatchlings may have a better chance of surviving after emergence because, due to longer crawl strides and swim strokes, they can crawl and swim faster, thereby avoiding predation more effectively (Janzen et al. 2000a, Gyuris 2000, Booth 2017, Le Gouvello et al. 2020).

The leatherback turtle population that nests at Playa Grande, which is part of the Parque Nacional Marino las Baulas (PNMB) in Guanacaste, Costa Rica, has decreased drastically since data collection first began at the end of the 1980s (Spotila et al. 2000). The main causes behind the population decline are interactions of adult turtles with fisheries and systematic illegal harvesting of eggs over many years (Spotila et al. 2000, Santidrián Tomillo et al. 2008). However, while the effects of temperature on hatching success and sex ratio are well studied in this population, there is still a gap in knowledge about how environmental and biotic factors affect hatchling size. The objectives of this study were to explore these effects and determine how egg size, temperature, and precipitation affect hatchling morphology in East Pacific leatherback turtles.

2. MATERIALS AND METHODS

2.1. Data collection

We collected data from leatherback turtle clutches relocated to a beach hatchery at Playa Grande (10° 20' 3" N, 85° 51' W), PNMB, Northwest Costa Rica, for nesting seasons between 2004–05 and 2018–19. Between October and December of each season, we collected clutches that would otherwise have been inundated had they been left *in situ* since they were laid below the high tide line. Eggs were collected while the turtle was laying them and were carried to a fenced hatchery where they were relocated at depths of 75 cm to the bottom of the nest. Maximum time between egg collection and relocation was 5 h. Before relocation, the number of eggs was counted, and 20 eggs were weighed individually. We placed one Type T thermocouple (24 gauge Cu–Cn) in the center of the clutch to take temperature measurements during development (Santidrián Tomillo et al. 2014). Because the daily variation in temperature is very low in leatherback nests (~0.1°C), we took temperature readings between 15:00 and 16:00 h every

other day during the incubation period using a Physitemp BAT-12 thermocouple reader ($\pm 0.1^\circ\text{C}$). We then estimated the mean temperature during development for each nest ($n = 124$).

We measured the straight carapace length, straight carapace width, head width, and mass of 20 hatchlings (or as many as possible if fewer than 20 hatchlings hatched) from each nest immediately after they emerged. We used a precision balance and digital vernier calipers, with precisions of 0.01 g and 0.1 mm, respectively, to weigh and measure the hatchlings.

We obtained precipitation data from the meteorological station in Liberia as a proxy for local climatic conditions. This is the closest station to PNMB (~50 km from the site at 144 m altitude).

Mean egg mass was calculated using the values from the 20 random eggs weighed at the time of relocation for each clutch. Hatching success was determined by dividing the number of empty shells (at least 50% of the shell left) by the total number of eggs in the clutch following Miller (1999). The total number of eggs in the clutch was obtained by adding the number of eggshells to the number of unhatched eggs. Finally, we constructed time series for mean incubation temperature, mean precipitation, hatching success, hatchling mass, straight carapace length, straight carapace width, and head width including all hatchery nests for which we had these data (208 nests; Table 1).

2.2. Statistical analyses

In order to determine which precipitation variables best predicted each dependent variable, we constructed generalized linear models (GLMs) and tested the relationship between hatchling sizes and accumulated precipitation over different time periods: (1) in September and October, which are the 2 rainiest months in northwest Costa Rica (and just at the onset of the nesting season) (rain_S&O), (2) in the month before eggs were laid, (rain-1), (3) in the 2 mo before eggs were laid (rain-2), (4) during the 2 mo of incubation (as the average incubation period of leatherbacks in the area is 2 mo) (rain_inc), (5) during the 2 mo of incubation and the month before (rain_inc-1), and (6) during the 2 mo of incubation and 2 mo before (rain_inc-2). All

models were compared using Akaike's information criterion (AIC).

GLMs were also used to assess the relationship between hatchling morphology, i.e. straight carapace length, straight carapace width, head width, and mass, and accumulated precipitation over different time periods, mean nest temperature, the interaction between nest temperature and precipitation, and average egg mass. Model details are provided in Table 2. In these analyses, we used average values of biometric measurements for each nest for which we had both hatchling measurements and temperature measurements (124 nests total; Table 1). We used the gamma distribution with the inverse link function because it accounts for increases in predictor variance with increases in the response variable. A goodness-of-fit test for overdispersion confirmed the adequacy of the families for each model. All statistical analyses were done using R (R Core Team 2018). The models were constructed using the GLM function in the 'stats' package (version 3.5.1) in R.

3. RESULTS

The best models for all dependent variables (hatchling mass, carapace length, carapace width, and head width) included egg mass, nest temperature, and precipitation (Table 2), and the precipitation

Table 1. Number of leatherback turtle nests placed in the hatchery (Total nests), number of nests with temperature measurements (Nests with temp), total number of hatchlings measured, mean nest temperature, mean incubation period, and mean hatching success of hatchery nests per season at Playa Grande, Costa Rica. -: not applicable

Season	Total nests	Nests with temp	Hatchlings	Mean nest temp. ($^\circ\text{C}$)	Mean incubation period (d)	Mean hatching success
2004–05	27	9	133	30.5	60.2	0.41
2005–06	32	10	187	30.4	63.3	0.49
2006–07	18	8	132	30.6	61.0	0.33
2007–08	29	6	19	28.9	64.6	0.58
2008–09	3	2	21	29.9	66.0	0.76
2009–10	22	5	91	31.5	57.6	0.48
2010–11	2	1	20	29.2	63.3	0.90
2011–12	4	4	80	29.7	63.3	0.62
2012–13	2	3	41	30.9	57.3	0.49
2013–14	14	13	224	31.3	57.7	0.46
2014–15	16	16	251	31.1	57.4	0.33
2015–16	8	17	98	32.3	57.4	0.15
2016–17	14	14	242	30.1	61.2	0.60
2017–18	12	10	170	30.5	58.7	0.42
2018–19	5	6	91	31.1	58.4	0.35
Total	208	124	1800	–	–	–

Table 2. Results of generalized linear models used to test the effect of egg mass (egg_mass), nest temperature (temp), and precipitation on mass, straight carapace length (SCL), straight carapace width (SCW), and head width (HW) of leatherback turtle hatchlings at Playa Grande, Costa Rica. The precipitation variables tested corresponded to precipitation accumulated over different time periods: September–October (rain_S&O), during incubation (rain_inc), 1 mo (rain-1) and 2 mo (rain-2) before incubation, 1 mo before and during incubation (rain_inc-1), and 2 mo before and during incubation (rain_inc-2). Models with the lowest Akaike's information criterion (AIC) value are marked in **bold**. Statistics for each variable (listed from highest to lowest Wald χ^2 value) are provided for the best models

Biometric variable	Model	AIC	Variable	Wald χ^2	p
SCL	SCL~ temp + rain_S&O + temp×rain_S&O + egg_mass	423.18			
	SCL~ temp + rain_inc + temp×rain_inc + egg_mass	414.12	temp	18.84	<0.001
			rain_inc	15.14	<0.001
			temp×rain_inc	15.11	<0.001
			egg_mass	5.86	<0.05
	SCL~ temp + rain-1 + temp×rain-1 + egg_mass	420.51			
	SCL~ temp + rain-2 + temp×rain-2 + egg_mass	420.64			
SCW	SCL~ temp + rain_inc-1 + temp×rain_inc-1 + egg_mass	417.12			
	SCL~ temp+ rain_inc-2 + temp×rain_inc-2 + egg_mass	417.51			
	SCW~ temp + rain_S&O + temp×rain_S&O + egg_mass	372.88			
	SCW~ temp + rain_inc + temp×rain_inc + egg_mass	364.44	egg_mass	13.61	<0.001
			temp×rain_inc	9.36	<0.01
			rain_inc	9.33	<0.01
			temp	8.61	<0.01
HW	SCW~ temp + rain-1 + temp×rain-1 + egg_mass	369.27			
	SCW~ temp + rain-2 + temp×rain-2 + egg_mass	369.99			
	SCW~ temp + rain_inc-1 + temp×rain_inc-1 + egg_mass	367.58			
	SCW~ temp+ rain_inc-2 + temp×rain_inc-2 + egg_mass	369.34			
	HW~ temp + rain_S&O + temp×rain_S&O + egg_mass	252.14	rain_inc	7.98	<0.01
			temp×rain_inc	7.48	<0.01
			temp	5.83	<0.05
Mass			egg_mass	5.66	<0.05
	HW~ temp + rain-1 + temp×rain-1 + egg_mass	251.71			
	HW~ temp + rain-2 + temp×rain-2 + egg_mass	252.57			
	HW~ temp + rain_inc-1 + temp×rain_inc-1 + egg_mass	248.28			
	HW~ temp+ rain_inc-2 + temp×rain_inc-2 + egg_mass	250.56			
	Mass~ temp + rain_S&O + temp×rain_S&O + egg_mass	479.67	egg_mass	14.05	<0.001
	Mass~ temp + rain_inc + temp×rain_inc + egg_mass	476.96	rain_inc	6.78	<0.01
		temp×rain_inc	6.31	<0.05	
		temp	0	>0.05	
Mass	Mass~ temp + rain-1 + temp×rain-1 + egg_mass	482.17			
	Mass~ temp + rain-2 + temp×rain-2 + egg_mass	482.38			
	Mass~ temp + rain_inc-1 + temp×rain_inc-1 + egg_mass	477.57			
	Mass~ temp+ rain_inc-2 + temp×rain_inc-2 + egg_mass	478.23			

variable that best explained all dependent variables was rain_inc (Table 2). For straight carapace length, nest temperature explained the greatest variability, followed by precipitation, the interaction between nest temperature and precipitation, and then egg mass (Table 2). Egg mass predicted the greatest variability in carapace width, followed by the interaction between nest temperature and accumulated precipitation, precipitation, and nest temperature (Table 2). In the case of head width, precipitation was the strongest independent variable, followed by the

interaction between nest temperature and precipitation, nest temperature, and then egg mass (Table 2). For hatchling mass, egg mass explained most of the variability within the model, followed by precipitation, the interaction between temperature and precipitation, and then temperature, which was not statistically significant (Table 2).

Mean nest temperature varied between seasons, ranging between 28.9°C (2007–08) and 32.3°C (2015–16) (Fig. 1). Seasons that were hotter and registered lower levels of precipitation corresponded with years

of lower hatching success (Fig. 1, Table 1). We found some variability in morphological measurements between years, with greater carapace length, carapace width, and mass corresponding with seasons with greater precipitation and cooler nest temperatures (Fig. 1). Head width, on the other hand, was relatively constant between seasons (Fig. 1).

Eggs of greater mass were correlated with hatchlings of greater mass ($n = 124$ nests, Wald $\chi^2 = 14.05$, $p < 0.001$, Fig. 2A), with longer ($n = 124$, $\chi^2 = 5.86$, $p < 0.05$, Fig. 2B) and wider carapaces ($n = 124$, $\chi^2 =$

13.61, $p < 0.001$, Fig. 2C), and wider heads ($n = 124$, $\chi^2 = 5.66$, $p < 0.05$, Fig. 2D). When precipitation was held constant, increases in nest temperature were associated with hatchlings of significantly shorter carapace lengths ($n = 124$, $\chi^2 = 18.84$, $p < 0.001$, Fig. 2F), narrower carapaces ($n = 124$, $\chi^2 = 8.61$, $p < 0.01$, Fig. 2G), and narrower heads ($n = 124$, $\chi^2 = 5.83$, $p < 0.05$, Fig. 2H). While hatchling mass decreased at greater nest temperatures, the relationship was not statistically significant ($n = 124$, $\chi^2 = 0.00$, $p > 0.05$, Fig. 2E). When nest temperature was held constant,

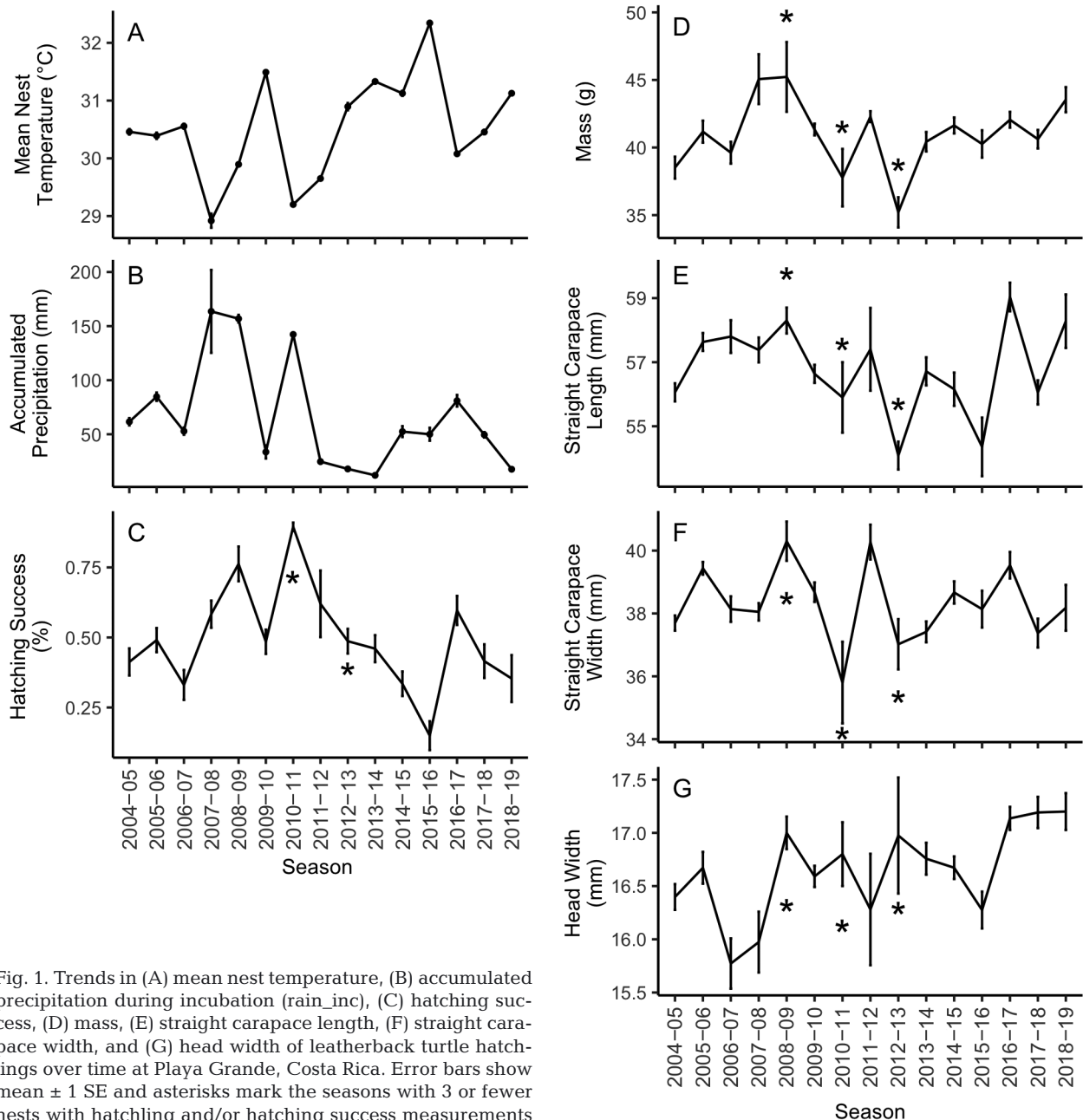


Fig. 1. Trends in (A) mean nest temperature, (B) accumulated precipitation during incubation (rain_inc), (C) hatching success, (D) mass, (E) straight carapace length, (F) straight carapace width, and (G) head width of leatherback turtle hatchlings over time at Playa Grande, Costa Rica. Error bars show mean \pm 1 SE and asterisks mark the seasons with 3 or fewer nests with hatchling and/or hatching success measurements

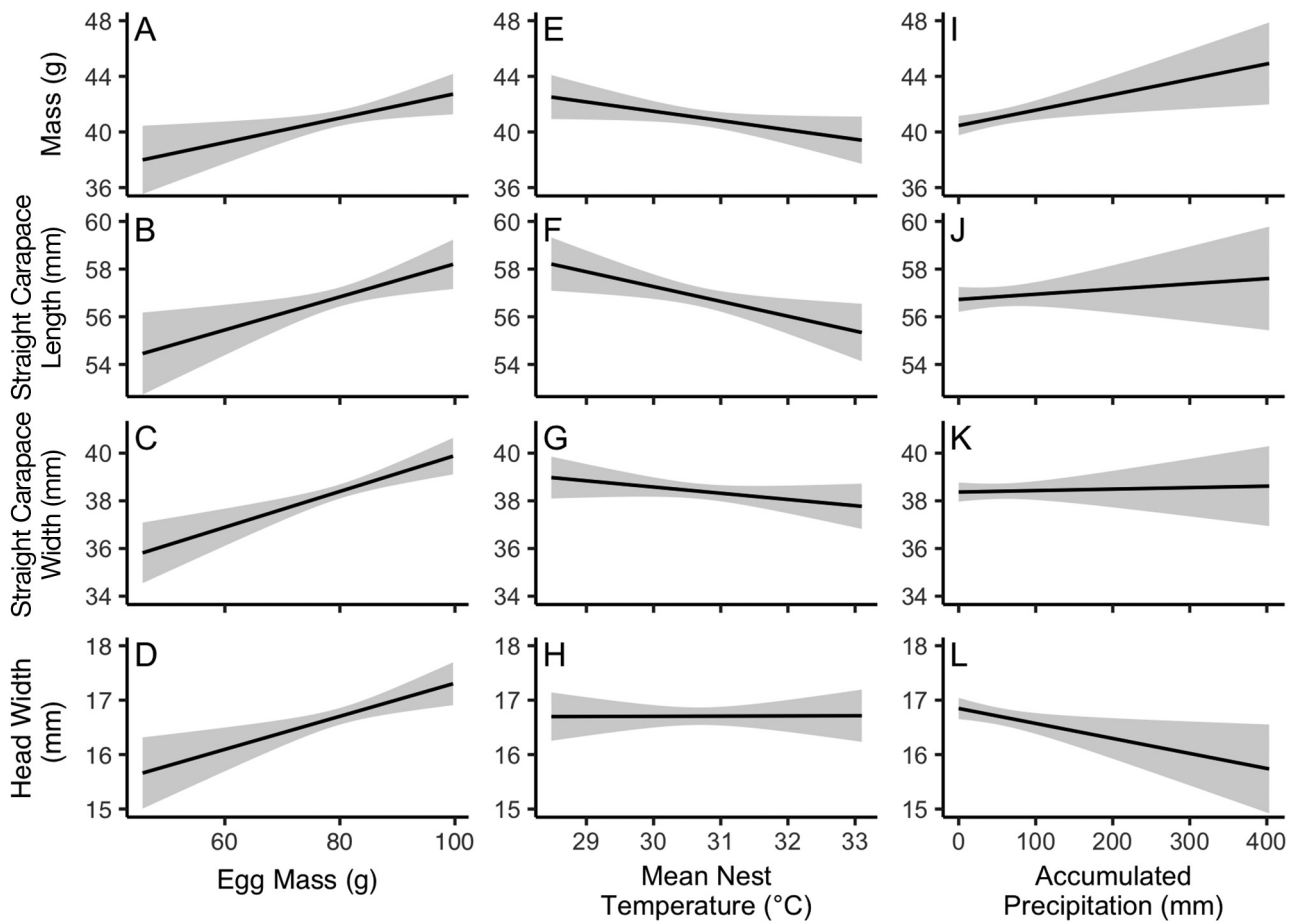


Fig. 2. Effects of (A–D) egg mass, (E–H) mean nest temperature during incubation, and (I–L) accumulated precipitation during the incubation period on leatherback biometric variables: hatchling mass, straight carapace length, straight carapace width, and head width. Shaded areas around the regression lines represent 95% confidence intervals

higher levels of precipitation were associated with significantly heavier hatchlings ($n = 124$, $\chi^2 = 6.78$, $p < 0.01$, Fig. 2I), with longer ($n = 124$, $\chi^2 = 15.14$, $p < 0.001$, Fig. 2J) and wider ($n = 124$, $\chi^2 = 9.33$, $p < 0.01$, Fig. 2K) carapaces. Conversely, increased precipitation was correlated to hatchlings with smaller heads ($n = 124$, $\chi^2 = 7.98$, $p < 0.01$, Fig. 2L).

On the other hand, the relationships between mean nest temperature and hatchling mass, carapace length, carapace width, and head width varied at varying quantities of precipitation during development (Fig. 3). As accumulated precipitation increased, the correlations between nest temperature and carapace length ($n = 124$, $\chi^2 = 15.11$, $p < 0.001$, Fig. 3B), carapace width ($n = 124$, $\chi^2 = 9.36$, $p < 0.01$, Fig. 3C), and head width ($n = 124$, $\chi^2 = 7.48$, $p < 0.01$, Fig. 3D) shifted from negative to positive. Conversely, as precipitation values increased, the relationship between temperature and mass changed

from a positive correlation to a negative one ($n = 124$, $\chi^2 = 6.31$, $p < 0.05$, Fig. 3A).

4. DISCUSSION

Egg-laying reptiles such as sea turtles rely on optimal levels of temperature, moisture, and gas exchange within their nests to produce a high number of hatchlings of good quality (Ackerman 1997, Hays et al. 2003, Dore 2005, Fuentes & Porter 2013, Santidrián Tomillo et al. 2014). Many sea turtle nesting beaches worldwide are projected to experience climate change that will affect sex ratios, clutch success, and hatchling morphology (Santidrián Tomillo et al. 2012, 2015b, Fuentes & Porter 2013, Telemeco et al. 2013a,b). The present study confirms that climate patterns at PNMB also have an impact on leatherback hatchling morphology.

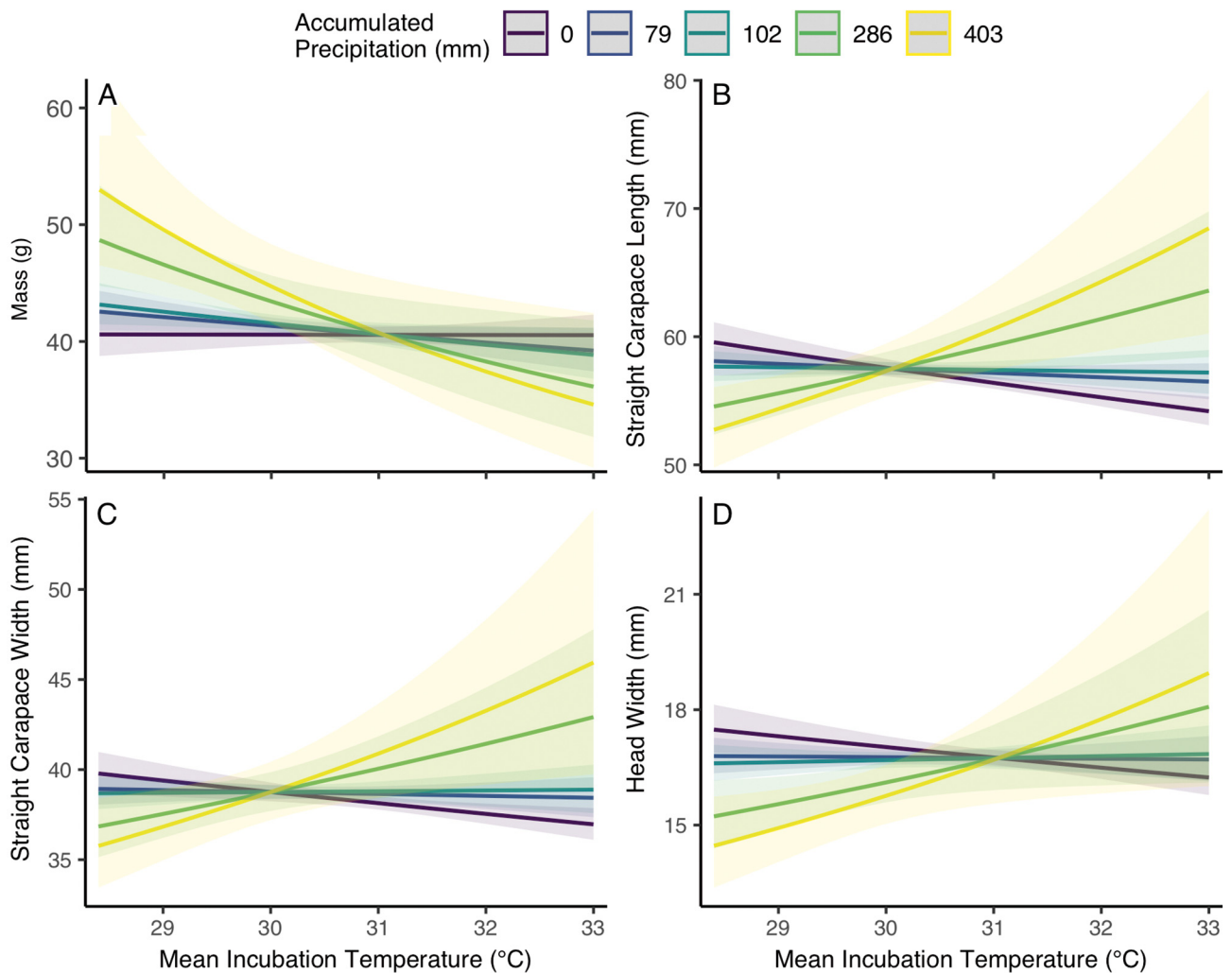


Fig. 3. Effects of mean nest incubation temperature on leatherback hatchling (A) mass, (B) straight carapace length, (C) straight carapace width, and (D) head width at varying quantities of accumulated precipitation during nest development

While egg mass was the most significant factor affecting hatchling carapace length and mass, temperature explained the majority of the variance for carapace width, and precipitation for head width. However, all statistical models were a better fit to data when egg mass, nest temperature, precipitation, and the interaction between nest temperature and precipitation were included, indicating that both a biotic factor and environmental conditions are important drivers of embryonic development and hatchling size at PNMB.

Hatchlings exposed to higher temperatures and lower precipitation levels during incubation were smaller, a pattern also found in other turtle species (Booth 2006, Burgess et al. 2006) that has been attributed to shorter incubation periods (Hewavisenthi & Parmenter 2001) and therefore less yolk being converted to hatchling tissue prior to hatching (Packard

et al. 1987, Booth 1998, Packard 1999). Studies have also found that lizards and other species of turtles whose eggs incubate for longer periods at lower temperatures absorb more water through their semi-permeable shells (Packard et al. 1987, Packard 1999, Booth et al. 2000), resulting in hatchlings of greater mass after emergence (Packard 1999, Booth et al. 2000). In fact, leatherback nests have shorter incubation periods at PNMB than at other locations (Santidrián Tomillo & Swiggs 2015), sometimes being as short as 55 d when climatic conditions are especially hot and dry (Table 2). These physiological responses to nest environment could explain why hatchlings at PNMB tended to be smaller when incubated at higher temperatures and lower precipitation.

The implications of small sizes in leatherback hatchlings have not been determined. However,

some studies have shown that small sea turtle hatchlings can exhibit lower locomotor performance than larger ones (Gyuris 2000, Janzen et al. 2000a, Burgess et al. 2006, Booth 2017, Le Gouvello et al. 2020). This could increase predation risk of hatchlings if poor locomotor performance increased the time hatchlings spend on the beach (Bustard 1972, Gyuris 2000, Janzen et al. 2000a,b, Booth 2017), which could be problematic for this population of leatherbacks. Furthermore, studies have shown that larger sea turtle hatchlings undergo less predation when crawling to the water (Janzen et al. 2000b) and in nearshore waters (Gyuris 2000), possibly because they may be discounted as prey by gape-limited predators (Bustard 1972, Booth 2017).

Mean nest temperature per season fluctuated between 28.9°C (2007–08) and 32.3°C (2015–16) at PNMB, which resulted in fluctuations in hatching success and hatchling morphology. As shown in previous studies conducted on *in situ* nests at PNMB (Santidrián Tomillo et al. 2014), seasons with higher nest temperatures corresponded with lower hatching success in hatchery nests. Here we found that these seasons also produced smaller hatchlings, which could contribute to the detrimental impact that hot seasons have on leatherback turtle hatchlings in northwest Costa Rica, if hatchling size impacts survivability. Further study is needed, however, on how leatherback hatchling morphology is related to post-emergence survival.

The Laúd OPO Network (2020) recently recommended a combination of decreasing fishery bycatch by 20% and increasing hatchling production by 7000 to 8000 individuals annually to achieve population recovery of East Pacific leatherback turtles. However, this scenario is difficult to achieve since climate projections show that temperature will increase and precipitation will decrease in Central America by the end of the 21st century (Intergovernmental Panel on Climate Change 2014, Santidrián Tomillo et al. 2015b). Should these climate projections come true, it will become increasingly difficult to accomplish the Laúd OPO's recommendations, as nests will increasingly produce fewer, and also smaller hatchlings, which could potentially have survival consequences.

As climate predictions become reality, endangered sea turtle populations are put under increasing pressure. In order to alleviate this pressure, it is of critical importance to understand the complex ways that weather patterns affect sea turtles. While this study reveals further issues associated with anthropogenic climate change, it more importantly points us towards new avenues for research and solutions. Some

climate mitigation studies have been conducted to test the effectiveness of shading and watering nests to decrease incubation temperatures (Wood et al. 2014, Hill et al. 2015). These methods could not only help increase the emergence success of a nest but also produce larger hatchlings that may be more likely to survive after emergence, if size is associated with fitness (Wood et al. 2014). Further study is required, however, to determine how climate patterns affect post-emergence survival rates specifically, and the differences in survival rates of female and male hatchlings, juveniles, and subadults. With this information, we can provide critically endangered populations of sea turtles such as the East Pacific leatherback turtle the best chance at recovery.

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