Original Research

Potential limitations of behavioral plasticity and the role of egg relocation in climate change mitigation for a thermally sensitive endangered species

Michael J. Liles1,10 | Tarla Rai Peterson2 | Jeffrey A. Seminoff3,10 | Alexander R. Gaos4,10 | Eduardo Altamirano5,10 | Ana V. Henríquez1,10 | Velkiss Gadea5,10 | Sofía Chavarría1,10 | José Urteaga6,10 | Bryan P. Wallace7,8,10 | Markus J. Peterson9

1 Asociación ProCosta, San Salvador, El Salvador
2 Department of Communication, Environmental Science and Engineering Program, University of Texas at El Paso, El Paso, Texas
3 National Oceanic and Atmospheric Administration – National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, California
4 Department of Biology, San Diego State University, San Diego, California
5 Fauna and Flora International, Managua, Nicaragua
6 School of Earth, Energy & Environmental Sciences, Stanford University, Stanford, California
7 Conservation Science Partners, Inc., Fort Collins, Colorado
8 Nicholas School of the Environment, Duke University Marine Lab, Beaufort, North Carolina
9 Department of Biological Sciences, University of Texas at El Paso, El Paso, Texas
10 Eastern Pacific Hawksbill Initiative, San Diego, California

Correspondence
Michael J. Liles, Asociación ProCosta, San Salvador, El Salvador.
Email: mjliles@procosta.org

Funding information
U.S. Fish and Wildlife Service; National Fish and Wildlife Foundation; United States Agency for International Development; SEE Turtles

Abstract
Anthropogenic climate change is widely considered a major threat to global biodiversity, such that the ability of a species to adapt will determine its likelihood of survival. Egg-burying reptiles that exhibit temperature-dependent sex determination, such as critically endangered hawksbill turtles (Eretmochelys imbricata), are particularly vulnerable to changes in thermal regimes because nest temperatures affect offspring sex, fitness, and survival. It is unclear whether hawksbills possess sufficient behavioral plasticity of nesting traits (i.e., redistribution of nesting range, shift in nesting phenology, changes in nest-site selection, and adjustment of nest depth) to persist within their climatic niche or whether accelerated changes in thermal conditions of nesting beaches will outpace phenotypic adaption and require human intervention. For these reasons, we estimated sex ratios and physical condition of hatchling hawksbills under natural and manipulated conditions and generated and analyzed thermal profiles of hawksbill nest environments within highly threatened mangrove ecosystems at Bahía de Jiquilisco, El Salvador, and Estero Padre Ramos, Nicaragua. Hawksbill clutches protected in situ at both sites incubated at higher temperatures, yielded lower hatching success, produced a higher percentage of female hatchlings, and produced less fit offspring than clutches relocated to hatcheries. We detected cooler sand temperatures in woody vegetation (i.e., coastal forest and small-scale plantations of fruit trees) and hatcheries than in other monitored nest environments, with higher temperatures at the deeper depth. Our findings indicate that mangrove ecosystems present a number of biophysical (e.g., insular nesting beaches and shallow water table) and human-induced (e.g., physical barriers and deforestation) constraints that, when coupled with the unique life history of hawksbills in this region, may limit behavioral compensatory responses by the species to projected temperature increases at nesting beaches. We contend that egg relocation can contribute significantly to recovery efforts in a changing climate under appropriate circumstances.
INTRODUCTION

Anthropogenic climate change is widely considered a major threat to global biodiversity (Foden et al., 2013; Parmesan & Yohe, 2003; Poloczanska et al., 2013), with 15%–37% of Earth’s species potentially “committed to extinction” by 2050 (Thomas et al., 2004). The ability of a species to exhibit compensatory responses to climate-driven environmental changes will determine its likelihood of survival; species more able to adjust to new environments or adapt to local climatic conditions will have a greater likelihood of persisting than those that cannot (Sinervo et al., 2010). Because the influence of climate change can vary among taxa and geographic regions (Parmesan, 2007), species may adapt in a variety of ways to mitigate unfavorable conditions (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012), including evolutionary changes (Shefferson, Mizuta, & Hutchings, 2017) and spatiotemporal shifts in behavior (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Yang & Rudolf, 2010).

In many reptiles, nest temperature regulates egg incubation duration, determines offspring sex, and affects progeny performance and survival (Bull, 1980; Van Damme, Bauwens, Braña, & Verheyen, 1992; Georges, 2013; Pike, 2014; Standora & Spotila, 1985). Adult female reptiles could respond to climate change by altering nesting range distribution, nesting phenology (i.e., timing of nesting), location of nest (e.g., amount of shade cover), and nest depth (Ewert, Lang, & Nelson, 2005; Pike, 2013b; Rfsnider, Bodenstein, Reneker, & Janzen, 2013; Schwanz & Janzen, 2008). For instance, maternal nest-site choice can compensate for climatic variation among populations of the Australian water dragon (Physignathus lesueurii; Doody et al., 2006). Similarly, behavioral plasticity in painted turtles (Chrysemys picta bellii) can allow females to match shade cover over nests with prevailing environmental conditions to influence the sex ratio of offspring (Rfsnider & Janzen, 2012).

Sea turtles are long-lived, late-maturing species that exhibit temperature-dependent sex determination (TSD). Pivotal temperature (i.e., temperature that produces 50% of each sex; Yntema & Mrosovsky, 1980) is relatively conserved among sea turtle species and is centered within a transitional range of temperatures (TRT; −1–3°C) that generally produce mixed sex ratios, where values above or below the narrow width of the TRT produce only one sex (Mrosovsky & Pleau, 1991; Wibbels, 2003). Successful egg development in sea turtles must occur between 25°C and 35°C (Ackerman, 1997), and temperature variations of −1°C can markedly skew hatchling sex ratios (Mrosovsky, Kamel, Diez, & Dam, 2009). Most studies report female-biased sex ratios (Broderick, Godfrey, & Godley, 2009; Wibbels, 2003), with some populations currently producing ≥90% female offspring (Broderick, Godley, Reece, & Downie, 2000; Godfrey, D’amato, Marcovaldi, & Mrosovsky, 1999; Marcovaldi, Godfrey, & Mrosovsky, 1997; Marcovaldi et al., 2014; Patino-Martinez, Marco, Quinones, & Hawkes, 2012b). Climate models predict levels of warming between +1.6°C and +4.0°C for Central America by 2100 (Magain, Marengo, & Boulanger, 2014), which would place additional thermal stress on embryonic development that may be nearing lethal thresholds with increasing frequency in many populations (Pike, 2014; Santidrián Tomillo et al., 2012; Valverde, Wingard, Gómez, Tordoír, & Orrego, 2010).

Given their complex life histories and reliance on marine and terrestrial habitats during their lifecycle, it is unclear how sea turtles will respond to climate-driven change in these environments. Changes in nesting phenology of sea turtles have been observed in multiple locations worldwide (Dalleau et al., 2012; Neeman, Robinson, Paladino, Spotila, & O’connor, 2015; Weishampel, Bagley, Ehrhart, & Weishampel, 2010), and further shifts in global distributions of nesting are forecasted (Pike, 2013a, 2013b). Additionally, because TSD and thermal thresholds of embryonic development are highly conserved among sea turtle species (Davenport, 1997; Wibbels, 2003), female turtles could potentially alter nest depth or site on a beach to mitigate increased temperatures (Roosenburg, 1996). Regardless, whether behavioral plasticity in nesting will enable sea turtles to meet the challenges posed by climate change remains uncertain (Hamann et al., 2010; Hawkes, Broderick, Godfrey, & Godley, 2007).

Given potential limitations of plastic compensatory responses of sea turtles to accelerated changes in thermal conditions of nesting beaches, it is possible that sea turtles will be unable to adapt quickly enough to offset negative consequences to population demographics. In such cases, human intervention may be required to ensure population persistence. Relocation of sea turtle eggs as a management strategy used to increase hatching productivity and enhance population recovery is ubiquitous worldwide (Chacón-Chaverri & Eckert, 2007; Formia, Tiwari, Fretey, & Billes, 2003; Garcia, Ceballos, & Adaya, 2003; Naro-Maciel, Mrosovsky, & Marcovaldi, 1999; Patino-Martinez, Marco, Quinones, & Hawkes, 2012b). By utilizing internationally recognized best practices throughout the egg relocation process (Eckert et al., 1999), many of the concerns about possible undesired biological outcomes (Mrosovsky, 2006; Pilcher & Enderby, 2001; Prichard, 1980) can be avoided or mitigated (Kornaraki, Matossian, Mazaris,
Because temperatures are predicted to increase substantively in Central America over a relatively short period, the influence of sea turtle egg relocation on the thermal regimes of nest environments, primary sex ratios, and hatchling fitness compared with in situ clutches is a top research priority, particularly for severely depleted populations of highly endangered species.

Critically endangered hawksbill turtles (*Eretmochelys imbricata*) in the eastern Pacific Ocean belong to one of the least resilient (Fuentes, Pike, Dimatteo, & Wallace, 2013) and most threatened marine turtle regional management units (RMU) in the world (Wallace et al., 2011), with fewer than 700 adult females nesting along 15,000 km of Latin American coastline (Gaos et al., 2017). Further, >70% of this nesting activity is concentrated on low-relief beaches in mangrove estuaries at Bahía de Jiquilisco in El Salvador and Estero Padre Ramos in Nicaragua (Gaos et al., 2017; Liles, Peterson, Seminoff, et al., 2015b)—ecosystems that are particularly vulnerable to increasing global temperatures and sea-level rise (Gilman, Ellison, Duke, & Field, 2008).

In this study, we investigated whether behavioral plasticity in this species is likely to be able to compensate for projected climate change and what the role of egg relocation may be as a mitigation strategy. The objectives of our study were to (a) estimate sex ratios and physical condition of hatchling hawksbills under natural and manipulated conditions (Figure 1) and (b) generate and analyze thermal profiles of nest environments. Our results provide the first empirical assessment of the efficacy of nest protection strategies for this severely depleted RMU. Based on our findings, we offer recommendations for mitigation strategies that complement potential plastic adaptive responses to climate change demonstrated by nesting hawksbills in mangrove ecosystems.

### 2 | MATERIALS AND METHODS

Our study was conducted at Bahía de Jiquilisco (13°13'N, 88°32'W) in El Salvador and Estero Padre Ramos (12°48'N, 87°28'W) in Nicaragua, which are located on the western and eastern borders of Gulf of Fonseca on the Pacific coast of Central America, respectively (Figure 2). Hawksbill nesting occurs primarily during the rainy season between May and September, with a peak in June and July. Contrary to typical contiguous open-coast beaches used by nesting hawksbills in other oceanic regions (Loop, Miller, & Limpus, 1995; Mrosovsky, 2006), hawksbills at these two sites nest on low-relief beaches scattered within mangrove estuaries (Gaos et al., 2017; Liles, Peterson, Seminoff, et al., 2015b).

Bahía de Jiquilisco is located on the south-central coast of El Salvador and has hawksbill nesting habitat (42.1 km) comprised of eight distinct fine-grained sand beaches with three hatcheries and one in situ nest protection area (Figure 2). A fragmented mosaic of second-growth coastal forest and small-scale fruit tree plantations 10–15 m wide from the high water line is present at most nesting beaches (Liles, Peterson, Seminoff, et al., 2015b). Moderate development exists in some nesting areas, particularly along eastern and western Punta San Juan, eastern and western Isla Madresal, and northern Isla San Sebastian.

Estero Padre Ramos is situated on the northwestern Pacific coast of Nicaragua and consists of eight distinct fine-grained sand beaches (12.8 km), with one hatchery and one in situ nest protection area (Figure 2). Intact secondary coastal forest extends >100 m landward from the high water line at most beaches (Liles, Peterson, Seminoff, et al., 2015b). Nesting areas have experienced relatively minimal development, with Padre Ramos most impacted.
2.1 | Nest distribution and protection strategies

Beach patrols were conducted from 1 April to 15 October 2011–2015 at Bahía de Jiquilisco and 1 May to 15 October 2010–2015 at Estero Padre Ramos. Project personnel and a network of >200 trained local egg collectors monitored nesting habitat continually from 18:00 to 06:00 daily by foot and boat in search of female hawksbills (~50% detection) and nests at both sites. Because of depressed socioeconomic conditions of coastal communities in both countries, local residents consider hawksbill eggs an economic resource, resulting in collection of nearly 100% of eggs (Liles et al., 2016; Liles, Peterson, Lincoln, et al., 2015a). Consequently, conservation organizations purchase eggs encountered and/or collected by local residents for protection to prevent their sale.

### Table 1

| Site Hatchery     | Year     | Size (m²) | Shade (%) | Shading materials |
|-------------------|----------|-----------|-----------|-------------------|
| Bahía de Jiquilisco |          |           |           |                   |
| Punta San Juan    | 2011     | 100       | 50        | PL                |
|                   | 2012–2014| 100       | 96.3      | SC; FC            |
|                   | 2015     | 100       | 100       | SC; FC            |
| La Pirraya        | 2011     | 50        | 70        | SC                |
|                   | 2012–2013| 50        | 84.5      | SC; FC            |
| Las Isletas       | 2013–2014| 50        | 90.1      | SC; FC            |
|                   | 2015     | 50        | 100       | SC; FC            |
| Estero Padre Ramos|          |           |           |                   |
| Punta Venecia     | 2010–2011| 125       | 100       | SC; FC            |
|                   | 2012–2015| 125       | 77.7      | SC; FC            |

Note. FC: forest canopy; PL: palm leaves; SC: shade cloth.

**FIGURE 3** Estimated hawksbill hatchling sex ratios at Bahía de Jiquilisco, El Salvador (2011–2015) and Estero Padre Ramos, Nicaragua (2010–2015). (a, b) Bimonthly frequency distribution of hawksbill nesting (gray bars) and estimated offspring sex ratios from three nest protection strategies (lines) at Bahía de Jiquilisco, (n = 835 clutches) and Estero Padre Ramos, (n = 1,196 clutches), respectively. (c, d) Annual mean (±SD) estimated offspring sex ratios from each nest protection strategy at Bahía de Jiquilisco and Estero Padre Ramos, respectively.
for human consumption. Each nesting season ~10% of hawksbill clutches typically are protected in situ via agreements with local residents to leave eggs in place, and ~90% of clutches are relocated to nearby areas of the beach or to hatcheries to avoid human depredation (Liles et al., 2016; Liles, Peterson, Lincoln, et al., 2015a).

The protection strategy employed for encountered nests depended on the likelihood of predation at the original site of egg deposition, the location of the nest, and the year at each site. At Bahía de Jiquilisco during 2011-2015, clutches deposited at the in situ protection area were not manipulated; however, we buried a surface-enclosed wire mesh cylinder (diameter, 50 cm; height,
60 cm) around each clutch at a depth of ~55 cm after oviposition had completed to reduce the probability of egg predation; we removed this barrier three days prior to the estimated date of hatching or when a depression in the sand was observed. Clutches deposited at beaches ≤3 km from the in situ protection area were relocated to the in situ protection area for protection, except during 2013–2015, when clutches were relocated to a hatchery. We relocated remaining clutches to the nearest hatchery, depending on the location of deposition (Table 1). At Estero Padre Ramos during 2010–2015, we did not manipulate clutches deposited at the in situ protection area. We relocated all clutches deposited at other beaches to a hatchery (Table 1), except during 2010 and 2011, when some clutches were relocated to an area of beach near the hatchery because the hatchery had reached capacity or was not yet operational.

For clutches relocated on the beach or to a hatchery, we measured the dimensions of original nest cavities and attempted to emulate these dimensions in artificial nests. We relocated most clutches <12 hr after deposition to minimize movement-induced mortality during transfer and reburial (Limpus, Baker, & Miller, 1979).

### 2.2 | Hatchling sex ratios and physical condition

Although direct methods for estimating hatchling sex ratios, such as histological evaluation of gonads, are highly accurate for sexing individual hatchlings, they are logistically infeasible to perform on endangered species. Indirect methods—including nest temperature and incubation duration—are reliable proxies when direct methods are infeasible (Wibbels, 2003). Because financial and logistical constraints prohibited us from recording nest temperatures at Estero Padre Ramos in 2010–2011, we used incubation duration values obtained for offspring-producing nests to estimate primary sex ratios at both sites to provide results that are commensurable across sites and among years.

We used published data for hawksbills that related incubation duration to sex ratio based on constant temperature incubator experiments to convert the incubation duration of each clutch into hatchling sex ratio (Godfrey et al., 1999). For incubation duration calculations, the incubation period was calculated as the number of days between the date and hour of clutch deposition and the date and hour of first hatching emergence. For nests where the date of emergence was unavailable (n = 50 nests, 2.5% of total) or where no hatchlings emerged but were found alive during exhumation (n = 30 nests, 1.5% of total), we used the average incubation duration of the nest protected using the same strategy immediately before and after the nest without date of emergence or with live hatchlings that did not emerge. We used a one- to four-day correction factor for the hatching-to-emergence interval in overall hatchling sex ratio calculations to establish a range of mean values that accounts for potential differences in the amount of time it takes a hatchling to emerge from the nest after hatching, which would affect incubation duration estimates (Godfrey et al., 1999; Godfrey & Mrosovsky, 1997). We calculated the overall sex ratio for each protection strategy within and across sites, and among years, and for specific comparisons among nest protection strategies and between sites, we used a three-day correction factor based on nests that showed a marked temperature signal at hatching (mean = 2.9 ± 0.2 days, n = 3; King, Cheng, Tseng, Chen, & Cheng, 2013).

Hawksbill nests at Bahía de Jiquilisco and Estero Padre Ramos hatch about 55–70 days after egg deposition. For clutches protected during the nesting season, successful nests were excavated within 48 hr of first hatching emergence to evaluate hatching success and failed nests were excavated on day 70 of incubation to identify potential causes of nest failure. We recorded the following metrics for reproductive output and hatching physical condition for each clutch: size (i.e., total number of eggs), hatching success (i.e., proportion of eggs that produced live hatchlings that emerged or were found in the nest during exhumation), and straight carapace length of hatchlings measured with calipers (Bahía de Jiquilisco, Neiko Tools, Taiwan; Estero Padre Ramos, Wilmar Corp, Tukwila, WA, USA) and hatchling mass using a digital scale (Bahía de Jiquilisco, American Weigh Scales, Norcross, GA, USA) and a spring scale (Estero Padre Ramos, Wilmar Corp, Tukwila, WA, USA).

### 2.3 | Thermal profiles of sand and nests

To measure intrabeach variation in temperature during the hawksbill nesting season, we divided the beach into four zones from ocean to forest, based on vegetative cover: (a) open sand (no vegetation), (b) nonwoody vegetation (herbaceous vegetation), (c) woody vegetation border (near the forest or plantations, but not completely surrounded by trees), and (d) woody vegetation (surrounded by trees; Liles, Peterson, Seminoff, et al., 2015b). We buried HOBO U22 data loggers (Water Temp Pro v2, Onset Computer Corporation, Bourne, MA, USA) in each of the four beach zones at two sand depths (30 and 60 cm), which are near the upper and lower range of hawksbill nest depths, respectively (Kamel & Mrosovsky, 2006a). At Bahía de Jiquilisco during 2012–2015, data loggers (hereafter referred to as “loggers”) were buried in beach zones along three transects, each separated by 500 m. Not all beach zones were present along each transect, which resulted in one or two paired-logger sites per zone per year. At Estero Padre Ramos during 2015, loggers were buried in four beach zones (n = 1 paired-logger site per zone). To assess the effects of deforestation on thermal conditions of nesting beaches (Kamel & Mrosovsky, 2006a), we placed loggers in areas cleared of vegetation at Bahía de Jiquilisco in 2012–2015 (n = 3 paired-logger sites per year) and at Estero Padre Ramos in 2015 (n = 1 paired-logger site). Loggers had an accuracy of ±0.2°C (per manufacturer specifications) and recorded the temperature every 30 min. We averaged recorded values to give a mean daily temperature for each logger, which facilitated comparisons with previous studies (e.g., Glen & Mrosovsky, 2004; Kamel & Mrosovsky, 2006b; Hawkes et al., 2007). Loggers that were stolen (n = 4 at Estero Padre Ramos), lost due to beach erosion (n = 4 at Bahía de Jiquilisco), or did not function properly during data collection (n = 4 at Bahía de Jiquilisco) were excluded from analyses. The stolen loggers at Estero Padre
| Site strategy          | Min temp (°C) | Max temp (°C) | Mean temp (°C) | Mean temp, TSP (°C) | Duration (days) | Nest depth (cm) | Hatching (%) | Female (%) | Mass (g) | Length (cm) |
|------------------------|---------------|---------------|----------------|---------------------|----------------|----------------|--------------|------------|----------|-------------|
| **Bahía de Jiquilisco** |               |               |                |                     |                |                |              |            |          |             |
| In situ                | 26.9 ± 1.7 (23) | 34.6 ± 1.3 (23) | 30.9 ± 1.1 (23) | 30.6 ± 1.4 (23) | 54.3 ± 3.9 (44) | 38.2 ± 3.2 (58) | 37.7 ± 31.1 (58) | 88.9–96.2 (44) | 10.78 ± 1.2 3 (625) | 3.75 ± 0.15 (601) |
| Relocated on beach     | 26.6 ± 0.7 (12) | 35.5 ± 1.9 (12) | 31.0 ± 0.1 (12) | 30.6 ± 1.0 (12) | 55.5 ± 3.7 (34) | 36.7 ± 3.3 (46) | 39.5 ± 32.2 (46) | 84.5–95.5 (34) | 11.44 ± 1.22 (420) | 3.75 ± 0.17 (491) |
| Hatchery               | 26.9 ± 1.3 (144) | 33.7 ± 1.7 (144) | 30.2 ± 1.1 (144) | 29.8 ± 1.1 (144) | 58.4 ± 4.6 (627) | 38.7 ± 3.2 (731) | 55.8 ± 33.1 (731) | 66.9–83.9 (627) | 11.19 ± 1.22 (10,930) | 3.76 ± 0.19 (9,355) |
| Total                  | 26.9 ± 1.3 (179) | 34.0 ± 1.7 (179) | 30.3 ± 1.1 (179) | 29.9 ± 1.2 (179) | 58.0 ± 4.7 (705) | 38.5 ± 3.2 (835) | 53.8 ± 33.4 (835) | 68.6–84.9 (705) | 11.18 ± 1.23 (11,975) | 3.76 ± 0.19 (10,447) |
| **Estero Padre Ramos** |               |               |                |                     |                |                |              |            |          |             |
| In situ                | 27.6 ± 1.5 (21) | 34.1 ± 1.2 (21) | 30.8 ± 0.9 (21) | 30.7 ± 1.2 (21) | 57.2 ± 3.5 (91) | 40.5 ± 4.5 (50) | 50.2 ± 28.1 (93) | 68.1–88.3 (91) | 11.21 ± 1.29 (448) | 3.66 ± 0.17 (386) |
| Relocated on beach     | –             | –             | –              | –                   | 61.3 ± 4.3 (68) | 43.8 ± 4.9 (25) | 50.3 ± 31.2 (77) | 32.3–58.7 (68) | 12.31 ± 1.53 (807) | 3.68 ± 0.16 (837) |
| Hatchery               | 27.8 ± 1.4 (74) | 33.5 ± 1.4 (74) | 30.6 ± 1.0 (74) | 30.3 ± 1.0 (76) | 57.7 ± 5.7 (981) | 41.7 ± 5.2 (926) | 61.1 ± 26.8 (1,026) | 66.0–78.8 (981) | 11.88 ± 1.52 (15,741) | 3.70 ± 0.18 (15,791) |
| Total                  | 27.8 ± 1.4 (95) | 33.7 ± 1.4 (95) | 30.7 ± 0.1 (95) | 30.3 ± 1.1 (97) | 57.9 ± 5.6 (1,140) | 41.7 ± 5.2 (1,001) | 59.6 ± 27.5 (1,196) | 64.2–78.3 (1,140) | 11.88 ± 1.52 (16,996) | 3.70 ± 0.18 (17,014) |

aValues in parentheses represent the number of clutches. bTSP, thermosensitive period. cValues in parentheses represent the number of hatchlings. dRange of mean values including 1- to 4-day correction factor for hatchling emergence. eExcludes year 2013–2014. fExcludes years 2012–2015.
**TABLE 3** Two-way ANOVA results for differences in each of six incubation regime variables among three nest protection strategies (in situ, relocated on beach, and hatchery) among years at Bahía de Jiquilisco, El Salvador (2011–2015), and Estero Padre Ramos, Nicaragua (2010–2015)

| Incubation regime source | Bahía de Jiquilisco | | Estero Padre Ramos | |
|--------------------------|---------------------|-----|---------------------|-----|
|                          | df | SS  | MS   | F      | p     | df | SS  | MS   | F      | p     |
| Minimum temperature      |    |     |      |        |       |    |     |      |        |       |
| Strategy                 | 2  | 0.0134 | 0.0067 | 0.0038 | 0.9620 | 1  | 0.0068 | 0.0068 | 0.0039 | 0.9501 |
| Year                     | 4  | 13.2291 | 3.3073 | 1.8711 | 0.1177 | 3  | 36.6277 | 12.2092 | 7.1135 | 0.0002 |
| Error                    | 171 | 302.2566 | 1.7676 | 1.7676 |         | 90 | 154.4700 | 1.7163 |         |       |
| Total                    | 177 | 316.3711 | 1.7874 |         |         | 94 | 192.0848 | 2.0435 |         |       |
| Maximum temperature      |    |     |      |        |       |    |     |      |        |       |
| Strategy                 | 2  | 38.4874 | 19.2437 | 7.4344 | 0.0008 | 1  | 6.0188 | 6.0188 | 3.3209 | 0.0717 |
| Year                     | 4  | 30.4110 | 7.6028 | 2.9372 | 0.0221 | 3  | 10.0939 | 3.3647 | 1.8564 | 0.1427 |
| Error                    | 171 | 442.6272 | 2.5885 |         |         | 90 | 163.1187 | 1.8124 |         |       |
| Total                    | 177 | 520.3395 | 2.9398 |         |         | 94 | 177.7459 | 1.2526 |         |       |
| Mean temperature         |    |     |      |        |       |    |     |      |        |       |
| Strategy                 | 2  | 17.6325 | 8.8162 | 8.1319 | 0.0004 | 1  | 1.9680 | 1.9679 | 2.7767 | 0.0991 |
| Year                     | 4  | 7.7559 | 1.9390 | 1.7885 | 0.1333 | 3  | 27.1719 | 9.0573 | 12.7796 | <0.0001 |
| Error                    | 171 | 185.3908 | 1.0842 |         |         | 90 | 63.7860 | 0.7087 |         |       |
| Total                    | 177 | 210.7523 | 1.1907 |         |         | 94 | 91.6039 | 0.9745 |         |       |
| Mean temperature, TP     |    |     |      |        |       |    |     |      |        |       |
| Strategy                 | 2  | 19.4525 | 9.7262 | 7.1573 | 0.0010 | 1  | 5.8476 | 5.8476 | 6.5880 | 0.0119 |
| Year                     | 4  | 6.3286 | 1.5822 | 1.1643 | 0.3284 | 3  | 28.2800 | 9.4267 | 10.6203 | <0.0001 |
| Error                    | 171 | 232.3751 | 1.3590 |         |         | 90 | 79.8848 | 0.8876 |         |       |
| Total                    | 177 | 259.4069 | 1.4656 |         |         | 94 | 111.3887 | 1.1849 |         |       |
| Incubation duration      |    |     |      |        |       |    |     |      |        |       |
| Strategy                 | 2  | 726.7760 | 363.3880 | 18.3004 | <0.0001 | 2  | 513.6550 | 256.8275 | 20.6619 | <0.0001 |
| Year                     | 4  | 532.8525 | 133.2131 | 6.7087 | <0.0001 | 5  | 20.192.0880 | 4.038.4176 | 324.8930 | <0.0001 |
| Error                    | 694 | 13.800.4950 | 19.8568 |         |         | 1,132 | 14.070.7530 | 12.4300 |         |       |
| Total                    | 701 | 15.228.9990 | 21.7247 |         |         | 1,139 | 35.122.7930 | 30.8365 |         |       |
| Nest depth               |    |     |      |        |       |    |     |      |        |       |
| Strategy                 | 2  | 209.5189 | 104.7594 | 10.1693 | <0.0001 | 2  | 251.7260 | 125.8630 | 8.0948 | 0.0003 |
| Year                     | 4  | 72.9575 | 18.2394 | 1.7705 | 0.1327 | 5  | 11.188.3430 | 2.237.6686 | 143.9148 | <0.0001 |
| Error                    | 828 | 8,529.6924 | 10.3016 |         |         | 993 | 15.439.7250 | 15.5486 |         |       |
| Total                    | 834 | 8,774.2069 | 10.5206 |         |         | 1,000 | 26,804.0230 | 26.8040 |         |       |
Ramos resulted in loss of temperature data for the open sand zone and deforested area.

To protect hawksbill clutches deposited on beaches where in situ protection and relocation on the beach were infeasible, shaded hatcheries were constructed at nesting beaches at both sites that typically operated from 1 May to 31 October annually and whose dimensions varied according to the capacity required for relocated clutches (Table 1). We buried loggers in the center of each hatchery at the two depths at Bahía de Jiquilisco in 2012–2015 (n = 2 or 3 hatcheries) and at Estero Padre Ramos in 2015 (n = 1 hatchery; Table 1). Temperature was recorded every 30 min and then averaged to obtain a mean daily temperature for each logger. Loggers that malfunctioned during data collection (n = 2 at Bahía de Jiquilisco) were not included in analyses.

To measure temperature in hawksbill nests during the incubation period, we placed HOBO U22 or HOBO U23 (Pro v2 Temperature/Relative Humidity, Onset Computer Corporation, Bourne, MA, USA) loggers in the center of the egg mass of clutches incubated in situ, relocated on the beach, and in hatcheries at Bahía de Jiquilisco during 2011–2015 and Estero Padre Ramos during 2012–2015. Deployment of loggers was spread across the nesting season to represent the temporal distribution of nests (n = 2 to 14 nests per month per site). Loggers recorded the temperature at 2.5-min or at 5-min intervals, depending on the logger model, and remained in the nest during the entire incubation period until they were removed at post-hatching nest excavation. We calculated daily mean temperature for each logger, which was then used to calculate the mean nest temperature during the entire incubation period and the mean nest temperature for the middle third of incubation when offspring sex is determined (i.e., thermosensitive period; Rimblot, Fretay, Mrosovsky, Lescure, & Pieu, 1985).

2.4 | Shade cover in hatcheries

At Bahía de Jiquilisco (2011–2015) and Estero Padre Ramos (2010–2015), we shaded nests in hatcheries using a variety of methods that included palm leaves, shade cloth (Bahía de Jiquilisco: Saran Verde, Freund, San Salvador, El Salvador, 75% radiation block; Estero Padre Ramos: undetermined model, 75% radiation block), and natural forest canopy (Table 1). Shade cover from palm leaves and forest canopy over hatcheries was measured using a convex spherical densitometer (Ben Meadows, Janesville, WI, USA), except at Punta San Juan hatchery at Bahía de Jiquilisco in 2011 and Estero Padre Ramos in 2010–2011 (Figure 2), where palm leaf cover above nests was estimated and complete forest cover over the hatchery effectively represented 100% shading, respectively. The same shade cover value was used for a hatchery across years when it remained in same location as the previous year and no changes were made to the forest canopy nor the shade cloth.

2.5 | Statistical analyses

We used version 4.0.3 of Girondot’s (1999) method to convert incubation duration of hawksbill clutches protected at our sites into hatching sex ratios. Two-way analysis of variance (ANOVA) was used to test for differences among the three nest protection strategies in each of 10 parameters of incubation regime (i.e., nest temperature—minimum, maximum, mean of entire period, mean of thermosensitive period—during incubation, incubation duration, and nest depth) and hatching condition (i.e., hatching success, offspring sex ratios, hatching mass, and hatching length) at Bahía de Jiquilisco and Estero Padre Ramos, and among years. We also used a two-way ANOVA to test for differences in sand temperature within and among the six nest environments between logger depths and years at Bahía de Jiquilisco and within and among the four nest environments between logger depths at Estero Padre Ramos. For summary statistics, values are expressed as mean ± SD. We computed all analyses using JMP Pro 12.0.0 (SAS Institute, Cary, NC, USA), with an alpha level of 0.05 where relevant.

3 | RESULTS

3.1 | Nest distribution and protection strategies

We recorded 2,154 nesting events from a minimum of 366 individual hawksbills, representing 72.8% of total nests recorded in the eastern Pacific during 2010–2015 and 69.3% of total mature females identified in the entire eastern Pacific region (Gaos et al., 2017). Of these nests, 877 (40.7%) were located at Bahía de Jiquilisco (2011–2015) and 1,277 (59.3%) at Estero Padre Ramos (2010–2015). Most hawksbills nested between May and August at Bahía de Jiquilisco (96.4%, n = 845 clutches) and Estero Padre Ramos (96.3%, n = 1,230 clutches), with a peak in nesting occurring in June and July (Bahía de Jiquilisco, 69.9%, n = 613 clutches; Estero Padre Ramos, 68.1%, n = 869 clutches; Figure 3a,b).

Of 2,154 hawksbill clutches deposited at Bahía de Jiquilisco and Estero Padre Ramos, we protected 94.6% (n = 2,038) at both sites—153 (7.5%) were protected in situ, 123 (6.0%) relocated on the beach, and 1,758 (86.3%) relocated to hatcheries, with the remaining four clutches (0.2%) protected using other methods and not included in this study. The remaining 5.4% of clutches were depredated by humans or domestic animals. We recorded the temperature of 23 (39.7%) and 21 (22.6%) clutches protected in situ, 12 (21.1%) and 0 (0.0%) clutches relocated on the beach, and 144 (17.2%) and 74 (7.3%) clutches relocated to hatcheries at Bahía de Jiquilisco and Estero Padre Ramos, respectively.

3.2 | Incubation regime

Across sites, mean nest depth was 40.3 ± 4.7 cm (range = 27–61, n = 1,836 nests), with shallower depth in clutches protected in situ (39.3 ± 4.0 cm, n = 108) and relocated on the beach (39.2 ± 5.1, n = 71) than in hatcheries (40.4 ± 4.7 cm, n = 1,657). Nest depth was shallower at Bahía de Jiquilisco than Estero Padre Ramos (Table 2), with significant differences among protection strategies at both sites (Table 3).
| Hatchling condition source | Bahía de Jiquilisco | | | | | | Estero Padre Ramos | | | | | |
|---------------------------|--------------------|----------------|--------|----------------|--------------------|----------------|--------|----------------|--------------------|----------------|--------|----------------|
|                           | df | SS | MS | F | p | df | SS | MS | F | p |
| Hatching success          |    |    |    |   |   |    |    |    |   |   |
| Strategy                  | 2  | 2.1532 | 1.0766 | 11.2887 | <0.0001 | 2  | 1.5695 | 0.7848 | 10.7819 | <0.0001 |
| Year                      | 4  | 11.3926 | 2.8481 | 29.8639 | <0.0001 | 5  | 1.7672 | 0.3534 | 4.8559 | 0.0002 |
| Error                     | 827 | 78.9171 | 0.0954 | 1.188 | 86.4682 | 0.0728 |
| Total                     | 834 | 93.1719 | 0.1117 | 1.195 | 90.0317 | 0.0753 |
| Female hatchlings         |    |    |    |   |   |    |    |    |   |   |
| Strategy                  | 2  | 1.2751 | 0.6375 | 7.3120 | 0.0007 | 2  | 4.1300 | 2.0650 | 42.2478 | <0.0001 |
| Year                      | 4  | 2.9112 | 0.7278 | 8.3473 | <0.0001 | 5  | 84.6158 | 16.9232 | 346.2371 | <0.0001 |
| Error                     | 698 | 60.8585 | 0.0872 | 1.132 | 55.3292 | 55.3292 |
| Total                     | 704 | 65.5458 | 0.0931 | 1.139 | 144.9736 | 0.1273 |
| Hatchling length          |    |    |    |   |   |    |    |    |   |   |
| Strategy                  | 2  | 0.4086 | 0.2043 | 6.0778 | 0.0023 | 2  | 0.4543 | 0.2271 | 7.9771 | 0.0003 |
| Year                      | 4  | 7.2448 | 1.8112 | 53.8863 | <0.0001 | 5  | 51.5192 | 10.3038 | 361.8605 | <0.0001 |
| Error                     | 10,440 | 350.9056 | 0.0336 | 17.006 | 484.2393 | 0.0285 |
| Total                     | 10,446 | 358.3552 | 0.0343 | 17.013 | 536.5475 | 0.0315 |
| Hatchling mass            |    |    |    |   |   |    |    |    |   |   |
| Strategy                  | 2  | 127.6789 | 63.8395 | 46.1007 | <0.0001 | 2  | 129.2909 | 64.6455 | 32.2017 | <0.0001 |
| Year                      | 4  | 1,339.9367 | 334.9842 | 241.9039 | <0.0001 | 5  | 5,035.8213 | 1,007.1643 | 501.6963 | <0.0001 |
| Error                     | 11,968 | 16,573.0700 | 1.3848 | 16.988 | 34.103.7110 | 2.0075 |
| Total                     | 11,974 | 18,044.3540 | 1.5070 | 16.995 | 39,496.0340 | 2.3240 |
Overall, mean nest temperature during the entire incubation period was 30.4 ± 1.1°C (n = 274 clutches), with slightly higher temperatures in clutches protected in situ (30.7 ± 1.0°C, n = 44) than clutches relocated to hatcheries (30.3 ± 1.1°C, n = 218). Mean nest temperature during the middle third of the incubation period was likewise higher in clutches protected in situ (30.6 ± 1.3°C, n = 44) than clutches relocated to hatcheries (29.9 ± 1.1°C, n = 218; overall, 30.1 ± 1.2°C, n = 276). There was little difference in nest temperature between sites (Table 2), but significant differences among nest protection strategies at both sites (Table 3).

Mean incubation duration was 57.9 ± 5.2 days (n = 1,845 clutches) across sites, with shorter duration of clutches protected in situ (56.3 ± 3.9 days, n = 135) than those relocated on the beach (59.4 ± 4.9 days, n = 102) and in hatcheries (58.0 ± 5.3 days, n = 1,608). Incubation duration was similar at Bahía de Jiquilisco and Estero Padre Ramos (Table 2), but significant differences existed among protection strategies and years at both sites (Table 3). At Bahía de Jiquilisco, incubation duration was significantly shorter (t = 9.8898, df = 703, p < 0.0001) during the first half (1 April–15 July; 56.9 ± 3.6 days, n = 495 clutches) than the second half (16 July–31 October; 60.5 ± 5.7 days, n = 210) of the nesting season, whereas at Estero Padre Ramos, only marginal differences were detected (t = 0.9564, df = 1,138, p = 0.3391; first half, 57.8 ± 5.7 days, n = 656; second half, 58.1 ± 5.4 days, n = 484).

3.3 | Hatching production, sex ratios, and physical condition

Across sites, protected clutches had a mean size of 160.2 ± 37.8 eggs (range = 3–274, n = 2,031), a mean hatching success of 56.8 ± 30.2% (n = 2031), and produced 185,922 hatchlings. Hatching success was lower in clutches protected in situ (43.6 ± 30.0%, n = 153) than those relocated on the beach (46.2 ± 32.2%, n = 124) and in hatcheries (58.6 ± 29.7%, n = 1,757). There were larger clutches and lower hatching success at Bahía de Jiquilisco than Estero Padre Ramos (Table 2), with significant differences in hatching success among nest protection strategies and years at both sites (Table 4). At Bahía de Jiquilisco, hatching success was significantly higher (t = 2.4390, df = 833, p = 0.0149) during the first half (55.7 ± 31.8%, n = 559) than the second half (49.7 ± 35.8%, n = 276) of the nesting season, whereas at Estero Padre Ramos, it was only slightly higher (t = 1.3734, df = 1,197, p = 0.1699; first half, 60.6 ± 26.8%, n = 679; second half, 58.4 ± 28.5%, n = 520).

The overall range of means for the percentage of female hatchlings produced from protected clutches was 66.0 ± 37.6 to 81.0 ± 37.6% (n = 1,845), with a greater percentage of female hatching production from clutches protected in situ (86.9 ± 20.1%, n = 135) than those relocated on the beach (63.2 ± 35.2%, n = 102) and in hatcheries (76.4 ± 34.4%, n = 1,608). Of the hatchlings produced at both sites, there was a higher percentage of females at Bahía de Jiquilisco than Estero Padre Ramos (Table 2), with significant differences among protection strategies and years at both sites (Table 4). No correlation existed between male hatching production and nest depth for clutches protected in situ ($r^2 = 0.01, F_{1,92} = 1.16, p = 0.2840$). At Bahía de Jiquilisco, the percentage of female hatchlings produced was significantly higher (t = 10.3636, df = 705, p < 0.0001) during the first half (87.3 ± 23.8%, n = 495) than the second half (63.1 ± 36.7%, n = 210) of the nesting season, whereas at Estero Padre Ramos, there were negligible differences (t = 0.0903, df = 1,138, p = 0.9281; first half, 73.7 ± 36.7%, n = 656; second half, 73.5 ± 34.9%, n = 484).

Hatchlings had a mean carapace length of 3.72 ± 0.18 cm (n = 27,461) and mean body mass of 11.59 ± 1.45 g (n = 28,971) across sites. Hatching length was nearly identical among protection strategies (in situ, 3.71 ± 0.16 cm, n = 987; relocated on beach, 3.71 ± 0.17 cm, n = 1,277; hatchery, 3.72 ± 0.18 cm, n = 25,146), but hatching mass was less in clutches protected in situ (10.96 ± 1.27 g, n = 1,073) than those relocated on the beach (12.01 ± 1.49 g, n = 1,227) and in hatcheries (11.60 ± 1.45 g, n = 26,670). Hatchlings produced at Bahía de Jiquilisco were slightly larger but weighed less than at Estero Padre Ramos (Table 2), and there were significant differences in hatching length and mass among strategies and years at both sites (Table 4).

3.4 | Sand temperature in beach, deforested, and hatchery environments

Sand temperatures at all logger locations exhibited temporal and spatial variation at Bahía de Jiquilisco (2012–2015) and Estero Padre Ramos (2015). At Bahía de Jiquilisco, temperatures steadily decreased by 1–2°C over the hawksbill nesting season at 30- and 60-cm sand depths from April through October in beach zones and deforested areas, and from May through October in hatcheries (Figure 4a,c). Beach and hatchery sand temperatures at Estero Padre Ramos decreased from 33°C to 29°C in June, rose to near-initial levels during July through August, and then decreased by 1–2°C from September through October (Figure 4b,d).

Mean sand temperatures during the nesting season at Bahía de Jiquilisco were greater than the most conservative male-producing pivotal temperature estimate for hawksbills among studied hawksbill populations (29.7°C; Godfrey et al., 1999) in all nest environments at both sites, except woody vegetation and hatcheries (Figure 4e). Woody vegetation was >3°C cooler than open sand at Bahía de Jiquilisco and nonwoody vegetation at Estero Padre Ramos (Figure 4e,f). Deforested areas and woody vegetation at Bahía de Jiquilisco logged the highest (31.9 ± 1.7°C, n = 2,558 days) and lowest (28.5 ± 0.8°C, n = 853) mean seasonal temperatures, respectively, with hatchery temperatures falling between these values (29.6 ± 1.0°C, n = 1,514; Figure 4e).

Nonwoody vegetation and woody vegetation at Estero Padre Ramos had the highest (33.4 ± 1.1°C, n = 170) and lowest (30.2 ± 1.0°C, n = 170) seasonal mean temperatures, respectively, with intermediate hatchery temperatures (31.1 ± 1.0°C, n = 170; Figure 4f).

There were significant differences in temperature between sand depths in woody vegetation, deforested areas, and hatcheries and among years at Bahía de Jiquilisco (Table 5), with the 60-cm depth warmer than the 30-cm depth in woody vegetation (30 cm, 28.5 ± 0.9°C, n = 851 days; 60 cm, 28.6 ± 0.7°C, n = 768) and hatcheries (30 cm, 29.3 ± 0.9°C, n = 1,319; 60 cm, 29.8 ± 1.0°C, n = 1,514; Figure 4e). Similarly, at Estero Padre Ramos, we detected significant differences in temperature between sand depths in nonwoody
vegetation, woody vegetation, and the hatchery (Table 5), with the 60-cm depth warmer than the 30-cm depth in woody vegetation (30 cm, 30.0 ± 1.1°C, n = 170; 60 cm, 30.4 ± 0.9°C, n = 170) and the hatchery (30 cm, 30.7 ± 1.0°C, n = 170; 60 cm, 31.5 ± 0.7°C, n = 170; Figure 4f). In all nest environments, fluctuations in daily temperature were greater at the 30-cm than at the 60-cm depth, regardless of mean daily temperature (Figure 4a–d).

### DISCUSSION

Uncertainty exists regarding the ability of long-lived thermally sensitive reptiles, such as sea turtles, to exhibit compensatory responses to accelerated climate-driven environmental changes capable of offsetting negative consequences to population demographics (Hays, Mazaris, Schofield, & Laloë, 2017; Laloë, Cozens, Renom, Taxonera,
& Hays, 2017). For eastern Pacific hawksbills nesting in mangrove estuaries at Bahía de Jiquilisco, El Salvador, and Estero Padre Ramos, Nicaragua, our results demonstrate that clutches protected in situ incubated at higher temperatures, yielded lower hatching success, produced a higher percentage of female hatchlings, and produced less fit offspring than clutches relocated to hatcheries. Additionally, sand temperature data of nesting beaches indicate that most nest environments already surpass the pivotal temperature for hawksbills, with higher temperatures at the deeper depth in the coolest nest environments (i.e., woody vegetation and hatchery).

4.1 | Natural nests produce fewer males and less fit hatchlings

Hawksbill clutches incubated in beaches within mangrove estuaries at Bahía de Jiquilisco and Estero Padre Ramos had relatively low hatching success (56.8%) across all protection strategies compared to hawksbill nesting on open-coast beaches in the eastern Pacific (e.g., 64.5%, Gaos et al., 2017), Caribbean (e.g., 91.6%, Bjorndal, Carr, Meylan, & Mortimer, 1985; 84.5%, Horrocks & Scott, 1991; 78.6%, Ditmer & Stapleton, 2012), and Indo-Pacific (90.1% [emergence success], Limpus, 1980; 79.9% [emergence success], Loop et al., 1995; 82.4%, Dobbs, Miller, Limpus, & Landry, 1999; 85.2%, Hoenner et al., 2016). We suspect differences in overall hatching success reflect distinct biophysical conditions of beaches in mangrove estuaries, such as presence of extremely fine-grained sand. Because sand grain size affects water and gas flux (Ackerman, 1980), sand consisting of small particle sizes could have interstitial spacing and high water content that inhibits respiratory gas exchange of developing embryos (Ackerman, 1997), which could lower hatching success. For example, nesting beaches at Bahía de Jiquilisco consist of a high proportion (90.1%) of sand particle sizes measuring ≤0.125 mm (Y. Flores, unpublished data), which is substantially smaller than sand grain sizes reported for hawksbill nesting beaches in other geographic regions (Ditmer & Stapleton, 2012; Dobbs et al., 1999; Zare, Vaghefi, & Kamel, 2012).

We found significantly lower hatching success in clutches protected in situ (43.6%) than clutches relocated on the beach (46.2%) or in hatcheries (58.6%) at both sites (Table 4). This difference probably arises primarily from differences in microenvironmental conditions during incubation (Eckert & Eckert, 1990; Kornaraki et al., 2006; Revuelta et al., 2015), such as the amount of organic content (e.g., roots and leaves) in the sand, which is likely lower in hatcheries due to removal of organic material during hatchery preparation. This is consistent with hawksbill clutches in Antigua (Caribbean), where hatching success increased as a function of decreasing organic content in the sand (Ditmer & Stapleton, 2012). Hatchery preparation processes could further favorably alter conditions of nest environments by lowering sand compaction within the hatchery enclosure, which could facilitate respiratory gas exchange of developing embryos (Garrett, Wallace, Garner, & Paladin, 2010).

We estimate that hawksbill nesting beaches produced 66.0%–81.0% female hatchlings across nest protection strategies at our sites, with a slightly higher percentage of females produced at Bahía de Jiquilisco than Estero Padre Ramos (Table 2). Our results represent lower female-biased sex ratios than reported at many sea turtle nesting beaches in other ocean basins (Hawkes et al., 2009; Poloczanska, Limpus, & Hays, 2009; Wibbels, 2003), but female production was more pronounced in clutches protected in situ, with 88.9%–96.2% and 68.1%–88.3% females at Bahía de Jiquilisco and Estero Padre Ramos, respectively. Clutches relocated to hatcheries at Estero Padre Ramos experienced a significant shift in sex ratios from highly male-biased in 2010–2011 to highly female-biased in 2012–2015 (Figure 3d). This shift is likely due to a change in hatchery location from a site with 100% overstory vegetation cover to an area with less cover (77.7%; Table 1), combined with climatic factors—such as cooler ambient temperature and increased precipitation associated with La Niña—reflected by longer incubation durations across protection strategies at Estero Padre Ramos. We attribute the higher percentage of female hatchlings produced at Bahía de Jiquilisco primarily to the degraded condition of coastal forest at many beaches relative to the higher-quality habitat that is available to nesting turtles at Estero Padre Ramos (Liles, Peterson, Seminoff, et al., 2015b), including areas where clutches are protected in situ. Indeed, vegetation cover can predict nest temperatures (Kamel, 2013) and hatchling sex (Janzen, 1994), which highlights the importance of preserving and restoring natural vegetation cover at hawksbill nesting beaches.

Hatchling length and mass differed among nest protection strategies and among years (Table 4), with hatchlings that were smaller and weighed less from clutches protected in situ than clutches relocated on the beach or in hatcheries (Table 2). Previous studies indicate that nest temperature is inversely correlated with hatching body size, where warmer nests produce hatchlings with smaller carapaces and flippers, but that nest temperature did not influence hatchling mass (Booth, Feeney, & Shibata, 2013; Maulany, Booth, & Baxter, 2012; Wood, Booth, & Limpus, 2014). Hatchlings with larger carapaces and flippers are likely to crawl faster and employ more thrust while swimming than smaller hatchlings (Ischer, Ireland, & Booth, 2009; Janzen, Tucker, & Paukstis, 2000), which may allow them to more quickly navigate away from near-shore predators to offshore waters and thus increase their chance of survival (Booth, 2017; Wood et al., 2014).

It is unclear, however, whether increased carapace size and locomotor performance in hatchlings at open-coast beaches confer similar advantages to hatchlings at inshore beaches in mangrove estuaries. Ongoing research into dispersal patterns of hawksbill hatchlings in Bahía de Jiquilisco suggests that hatchling movements are regulated by tidal currents in the estuary, where turtles tend to passively drift camouflaged among floating debris (e.g., mangrove shoots and leaves) while transported by tidal currents (M. Liles, unpublished data). This behavior suggests that smaller hatchlings from warmer in situ nests may not necessarily be at a comparative disadvantage to larger hatchlings from clutches relocated on the beach and in hatcheries while inside mangrove estuaries, but could be at a disadvantage if transported outside the estuary and thence required to actively swim to encounter ocean currents.
4.2 | Warmer sand temperatures at the deeper depth

Our data on seasonal sand temperature in nest environments delineate temporal and spatial differences in hawksbill nesting environments at Bahía de Jiquilisco and Estero Padre Ramos. We found sand temperatures generally decreased from ocean to forest, with woody vegetation and hatcheries cooler than other nest environments (Figure 4e,f), which is consistent with thermal patterns reported for some hawksbill nesting beaches (Kamel, 2013; Kamel & Mrosovsky, 2006a), but contrasts with studies at other hawksbill nesting beaches that detected no difference between unshaded and shaded areas (Glen & Mrosovsky, 2004; Mrosovsky, Bass, Corliss, Richardson, & Richardson, 1992).

For most beach and hatchery environments at Bahía de Jiquilisco and Estero Padre Ramos, mean sand temperature was higher at the deeper depth (Figure 4e,f), which contrasts with the prevailing paradigm that temperatures are lower at deeper depths (Glen & Mrosovsky, 2004; Hill, Paladino, Spotila, & Santidrián Tomillo, 2015; Naro-Maciel et al., 1999). For example, Lalöe, Esteban, Berkel, and Hays (2016) found consistently cooler sand temperature at deeper depths along a hawksbill nesting beach on St. Eustatius Island (Caribbean), where temperature at 100 cm was 1°C cooler than at 40–60 cm. One potential explanation for warmer temperatures at the deeper depth at our sites is the presence of groundwater at a depth of <1 m during the nesting season. Because groundwater absorbs and redistributes geothermal heat as it flows horizontally (Cartwright, 1974), the temperature of shallow groundwater (<10 m) can be 1–2°C greater than the mean annual surface temperature (Anderson, 2005) which can be further amplified in heavily shaded areas (Lewis & Wang, 1998), such as in woody vegetation and hatchery environments at our sites (Figure 4e,f).

4.3 | Potential limitations of behavioral plasticity in climate change adaptation

Previous studies argue that sea turtles may adapt to climate change through nesting behavioral plasticity, including redistribution of nest depths (Limpus, 2006; Pike, 2013b; Schofield et al., 2010), shifts in nesting phenology toward cooler months (Patel et al., 2016; Saba, Stock, Spotila, Paladino, & Santidrián Tomillo, 2012; Weishampel, Bagley, & Ehrhart, 2004), changes in nest-site selection (Hawkes et al., 2007; Hays et al., 2001), and alteration of nest depth (Hays et al., 2001; Lalöe et al., 2016; Pike, 2013a). However, our findings indicate that mangrove ecosystems of Bahía de Jiquilisco and Estero Padre Ramos present a number of biophysical and human-induced constraints that, when coupled with unique life-history characteristics of eastern Pacific hawksbills, may limit behavioral compensatory responses by the species to projected temperature increases at nesting beaches.

Because >80% of female hawksbills in the eastern Pacific nest along low-relief beaches on islands and peninsulas within mangrove estuaries (Gaos et al., 2017; Liles, Peterson, Seminoff, et al., 2015b), climate-driven sea-level rise threatens viability of current nesting beaches. Global mean sea level is projected to rise between 0.26 and 0.98 m (Church, Clark, & Cazenave, 2013), but to as high as 1.14 m when accounting for Greenland and Antarctica ice loss (DeConto & Pollard, 2016), by 2100. Under sea-level rise scenarios of 0.1, 0.5, and 0.9 m, Fish et al. (2008) estimated that 4%, 26%, and 51% of total beach area, respectively, would be submerged from 11 low-elevation beaches (1.25–3.09 m) with gentle slope (1.8–5.8°) used by nesting hawksbills on Barbados (Caribbean), with similar estimates (i.e., 14%, 31%, and 51%, respectively) for 13 low-relief hawksbill nesting beaches on Bonaire (Caribbean; Fish et al., 2005). Given that most hawksbill nesting beaches at Bahía de Jiquilisco and Estero Padre Ramos have an elevation of ≤1 m above mean sea level with marginal slope (<2°), beach loss of 4%–51% likely represents a conservative estimate for our sites under sea-level rise scenarios of 0.1–0.9 m by 2100. Indeed, vulnerability of nesting beaches to sea-level rise was exemplified by a flooding event that occurred at Bahía de Jiquilisco in 2015, where all eight nesting beaches were temporarily inundated from extraordinarily high tides and precipitation, resulting in total mortality of 30 hawksbill clutches.

Strategies to mitigate beach loss from climate change include enforcement of existing construction setback regulations and prevention of coastal infrastructure that alter nesting areas (Fuentes, Fish, & Maynard, 2012). Although conservation setbacks can be an important tool for maintaining nesting beach integrity (e.g., Fish et al., 2008), and despite nominal protective measures that prohibit human use of beaches 100 m landward from the high tide line in Nicaragua (República de Nicaragua, 2009), most beaches at our sites are backed by human settlements, small-scale agriculture, or mangrove forests in the intertidal zone, which can restrict inland retreat of beaches. While the paleoenvironmental record indicates that mangroves have adjusted to sea-level changes over millennia through vertical sediment accretion and subsurface root accumulation (Ellison, 2008; Woodroffe et al., 2016), the current rate of sea-level rise likely will outpace gain in soil surface elevation, and in areas where physical barriers (e.g., aquaculture ponds, coastal infrastructure, and agricultural fields) prevent landward migration, such as at our sites, mangroves may submerge (LoveLock et al., 2015). Given that 90% (n = 564 clutches annually) of hawksbill reproductivity output in the eastern Pacific is concentrated at five nesting sites within only one degree latitude (12°35’–13°35’N; Gaos et al., 2017), highly specific biophysical (e.g., sand morphology and ocean currents) and human-induced (e.g., depredation and beach development) conditions govern viability of these areas as suitable nesting habitat, suggesting that latitudinal redistribution to exploit other Central American beaches where similar climatic patterns are projected to occur seems unlikely (Saba et al., 2012; Santidrián Tomillo et al., 2012).

Shifts in nesting phenology have been observed for some sea turtle populations (Azanza-Ricardo et al., 2017; Patel et al., 2016; Weishampel et al., 2004). Because sand temperatures at Bahía de Jiquilisco and Estero Padre Ramos generally decreased over the nesting season in all nest environments at both depths (Figure 4a–d), the decrease in
temperature between the beginning (April–May) and end (September–October) of the nesting season—which is reflected in shorter incubation durations and higher percentage of female hatchlings produced during the first half than the second half of the nesting season (Figure 3a,b)—suggests that hawksbills could respond to projected temperature increases by nesting later in the season to exploit cooler temperatures. Additionally, turtles that currently nest in September–October at both sites may have an adaptive advantage (Valladares et al., 2014), highlighting the importance of protecting the nests of these individuals, even if their numbers are relatively fewer during those later months.

Some turtle populations appear to be capable of spatially adapting nest placement to align the current thermal niche of the nest environment with changing climatic conditions, whereas others seem relatively inflexible. For example, female painted turtles from five distinct populations across their geographic range that were translocated to a common environment differed in choice of nesting date and nest depth, but did not differ in shade cover, resulting in similar incubation regimes across populations despite differences in local climate at their locations of origin (Refsnider & Janzen, 2012). In contrast, individual hawksbills in the Caribbean are highly consistent in their nest microhabitat preferences, including vegetative cover above nests within and between years (Kamel & Morosovsky, 2005, 2006b), suggesting that female hawksbills are relatively constrained in their ability to alter nesting behavior (Kamel, 2013). Although hawksbills at Bahía de Jiquilisco and Estero Padre Ramos are highly consistent in their selection of vegetative cover, they exhibit locally specific adaptations shaped by microhabitat differences at each site (Liles, Peterson, Seminoff, et al., 2015b). For example, nest placement by hawksbills at Bahía de Jiquilisco is restricted to the narrow tract of secondary forest measuring 10–15 m wide adjacent to the high water line at most beaches, whereas nest placement at Estero Padre Ramos extends nearly twice the distance inland within intact second-growth forest that is present >100 m landward from the high water line at most beaches (Liles, Peterson, Seminoff, et al., 2015b). Such adaptations may indicate the potential for development of compensatory responses to climate variability through nest-site choice.

However, mangrove ecosystems are among the most threatened tropical environments in the world, with deforestation rates as high as 3.6% per year in the Americas (Valiela, Bowen, & York, 2001), suggesting that future degradation of forest habitat may impair its ability to buffer against increasing temperatures (Patricio et al., 2017). Coastal forests at our sites are confronted with the persistent threat of conversion by competing land uses, and forests along nesting beaches at Bahía de Jiquilisco have already experienced substantial alteration that restricts nest-site selection by hawksbills (Liles, Peterson, Seminoff, et al., 2015b). Our findings suggest that inability to halt the continued fragmentation of intact woody vegetation will progressively replace cooler male hatching producing refugia (28.5°C) for naturally incubating clutches with markedly warmer woody vegetation border (30.2°C) and deforested (31.9°C) areas, increasing the probability of highly female-biased sex ratios (Poloczanska et al., 2009) and ultimately, climate-driven egg and hatching mortality (Santidrián Tomillo et al., 2012).

The ability of egg-burying species to alter nest depth to compensate for increasing temperatures has been advanced as a possible adaptive strategy, presumably under the basic assumption that nest environments become cooler with increasing depth (Davenport, 1989; Fuentes & Porter, 2013). Our results, however, indicate that adjustment of nest depth by hawksbills is unlikely to compensate for climate change in mangrove estuaries. First, we detected higher temperatures at the deeper depth in most nest environments at both sites (Figure 4e,f). Second, the water table is at a depth of 50–85 cm during the nesting season at many beaches, which can be expected to become shallower as sea levels rise and further constrict suitable nest environments (Pike, 2014). This likely explains, at least in part, why hawksbills construct shallower nest cavities at Bahía de Jiquilisco (38.2 cm) and Estero Padre Ramos (40.5 cm) than at open-coast nesting locations in the Caribbean (e.g., 47.0 cm, Kamel & Morosovsky, 2006a), Indo-Pacific (e.g., 45.3 cm, Loop et al., 1995), and Indian Ocean (e.g., 46.5 cm, Hitchins, Bourquin, Hitchins, & Piper, 2004). Finally, male hatching production at Bahía de Jiquilisco and Estero Padre Ramos is not correlated with nest depth for clutches protected in situ, suggesting that shifts in nesting phenology and nest-site choice may be more effective adaptive responses to a warming climate.

The accelerated rate at which climate change is projected to occur, together with other interacting anthropogenic threats, may outpace the biological capacity of sea turtles to adapt (Fuentes, Hamann, & Limpus, 2010). The inability of sea turtles to adaptively respond through behavioral or evolutionary mechanisms (e.g., adjust pivotal temperature; Davenport, 1989) would require that humans intervene to prevent local extinctions, such as poisoning, shading, and clutch relocation to modify sand temperatures and reduce egg and hatching mortality (Hill et al., 2015; Jourdan & Fuentes, 2015; Wood et al., 2014). Indeed, we found that hawksbill clutches relocated on the beach and protected in shaded hatcheries had higher hatching success, produced higher proportions of male offspring, and produced fitter hatchlings than clutches protected in situ at Bahía de Jiquilisco and Estero Padre Ramos. However, we are not suggesting egg relocation as a panacea that should be employed without careful consideration of local conditions, species biology, and conservation objectives. Previous studies have highlighted negative consequences of hatcheries using poor management practices, such as low hatching success (Boulon, Dutton, & Mcdonald, 1996), biased sex ratios of hatchlings (Morreale, Ruiz, Spotila, & Standora, 1982), and increased hatching mortality (Pitcher & Enderby, 2001). We contend, however, that egg relocation can contribute substantively to recovery efforts under appropriate circumstances. Our results underscore the importance of empirical assessments to evaluate potential mitigation strategies for severely depleted populations of highly endangered species that may be unable to respond sufficiently to climate change.

ACKNOWLEDGMENTS

We thank local egg collectors and residents of Bahía de Jiquilisco and Estero Padre Ramos for their trust and collaboration. We acknowledge
numerous people and organizations for their assistance with this study, including N. Sanchez, L. Manzanares, M. Godfrey, G. Serrano Liles, I. Yafiez, D. Melero, B. Nahill, T. Eguchi, P. Torres, C. Dueñas, M. Pico, E. Possardt, the Hawksbill Committees of Bahía de Jiquilisco and Estero Padre Ramos, and The Ocean Foundation. We are grateful for permits from the national environmental authorities in El Salvador (MARN) and Nicaragua (MARENA), and are indebted to the National Fish and Wildlife Foundation, U.S. Fish and Wildlife Service, SEE Turtles, and U.S. Agency for International Development for consistently funding hawksbill conservation initiatives that facilitated data collection for this study. We appreciate constructive comments on earlier drafts from three anonymous reviewers.

CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

MJL, TRP, JAS, ARG, BPW, and MJP conceived and designed the study. MJL, EA, AVH, VG, SC, and JU collected data. MJL and MJP carried out data analyses. MJL led writing of the manuscript with input and critical review from all authors.

DATA ACCESSIBILITY

Hawksbill hatching and temperature data can be accessed in the Dryad Digital Repository. https://doi.org/10.5061/dryad.33rq371.

ORCID

Michael J. Liles  https://orcid.org/0000-0002-0471-8816
Tarla Rai Peterson  https://orcid.org/0000-0002-2864-0013
Alexander R. Gaos  https://orcid.org/0000-0001-6100-7319
Bryan P. Wallace  https://orcid.org/0000-0001-9537-3501
Markus J. Peterson  https://orcid.org/0000-0001-6145-0134

REFERENCES

Ackerman, R. A. (1980). Physiological and ecological aspects of gas exchange by sea turtle eggs. American Zoologist, 20, 575–583. https://doi.org/10.1093/icb/20.3.575
Ackerman, R. A. (1997). The nest environment and the embryonic development of sea turtles. In P. L. Lutz, & J. A. Musick (Eds.), The Biology of Sea Turtles, Vol. 1 (pp. 83–106). Boca Raton, FL: CRC Press.
Anderson, M. P. (2005). Heat as a ground water tracer. Groundwater, 43, 951–968. https://doi.org/10.1111/j.1745-6845.2005.00052.x
Azanza-Ricardo, J., Ibarra Martín, M. E., González Sansón, G., Harrison, E., Medina Cruz, Y., & Bretos, F. (2017). Possible effect of global climate change on Caretta caretta (Testudines, Cheloniidae) nesting ecology at Guanahacabibes Peninsula. Cuba. Chelonian Conservation and Biology, 16, 12–19.
Bellard, C., Bertelsemier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. Ecology Letters, 15, 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x
Bjorndal, K. A., Carr, A., Meylan, A. B., & Mortimer, J. A. (1985). Reproductive biology of the hawksbill Eretmochelys imbricata at Tortuguero, Costa Rica, with notes on the ecology of the species in the Caribbean. Biological Conservation, 34, 353–368. https://doi.org/10.1016/0006-3207(85)90040-0
Booth, D. T. (2017). The influence of incubation temperature on sea turtle hatching quality. Integrative Zoology, https://doi.org/10.1111/1749-4877.12255
Booth, D. T., Feeeney, R., & Shibata, Y. (2013). Nest and maternal origin can influence morphology and locomotor performance of hatching green turtles (Chelonia mydas) incubated in field nests. Marine Biology, 160, 127–137. https://doi.org/10.1007/s00227-012-2070-y
Boulon, R. H., Dutton, P. H., & Mcdonald, D. L. (1996). Leatherback turtles (Dermochelys coriacea) on St. Croix, U.S. Virgin Islands: Fifteen years of conservation. Chelonian Conservation and Biology, 2, 141–147.
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. Marine Ecology Progress Series, 202, 273–281. https://doi.org/10.3354/meps202273
Bull, J. J. (1980). Sex determination in reptiles. The Quarterly Review of Biology, 55, 3–21. https://doi.org/10.1086/411613
Cartwright, K. (1974). Tracing shallow groundwater systems by soil temperatures. Water Resources Research, 10, 847–855. https://doi.org/10.1029/WR010i004p00847
Chacón-Chaverri, D., & Eckert, K. L. (2007). Leatherback sea turtle nesting at Gandoca Beach in Caribbean Costa Rica: Management recommendations from fifteen years of conservation. Chelonian Conservation and Biology, 6, 101–110. https://doi.org/10.2744/1071-8443(2007)6[101:LSTNAG]2.0.CO;2
Chen, I., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. Science, 333, 1024–1026. https://doi.org/10.1126/science.1206432
Church, J. A., Clark, P. U., Cazenave, A., et al. (2013) Sea level change. In: T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (pp. 1137–1216). Cambridge, UK and New York, NY, USA: Cambridge University Press.
Dalleau, M., Ciccone, S., Mortimer, J. A., Garnier, J., Benhamou, S., & Bourjea, J. (2012). Nesting phenology of marine turtles: Insights from a regional comparative analysis on green turtle (Chelonia mydas). PLoS ONE, 7, e46920. https://doi.org/10.1371/journal.pone.0046920
Davenport, J. (1989). Hawksbill turtle populations on Long Island, Antigua, West Indies. American Zoologist, 29, 575–583. https://doi.org/10.1093/icb/29.3.575
Deconto, R. M., & Pollard, D. (2016). Contribution of Antarctica to past and future sea-level rise. Nature, 531, 591–597. https://doi.org/10.1038/nature17145
Ditmter, M. A., & Stapleton, S. P. (2012). Factors affecting hatch success of hawksbill sea turtles on Long Island, Antigua, West Indies. Plos ONE, 7, e38472.
Dobbs, K. A., Miller, J. D., Limpus, C. J., & Landry, A. M. Jr (1999). Hawksbill turtle, Eretmochelys imbricata, nesting at Milman Island, northern Great Barrier Reef, Australia. Chelonian Conservation and Biology, 3, 344–361.
Doody, J. S., Guarino, E., Georges, A., Corey, B., Murray, G., & Ewert, M. (2006). Nest site choice compensates for climate effects on sex ratios in a lizard with environmental sex determination. Evolutionary Ecology, 20, 307–330. https://doi.org/10.1007/s10682-006-0003-2
Duputié, A., Rutschmann, A., Ronce, O., & Chaine, I. (2015). Phenological plasticity will not help all species adapt to climate change. Global Change Biology, 21, 3062–3073. https://doi.org/10.1111/gcb.12914
Jourdan, J., & Fuentes, M. M. P. B. (2015). Effectiveness of strategies at reducing sand temperature to mitigate potential impacts from changes in environmental temperature on sea turtle reproductive output. Mitigation and Adaptation Strategies for Global Change, 20, 121–133. https://doi.org/10.1007/s11027-013-9482-y

Kamel, S. J. (2013). Vegetation cover predicts temperature in nests of the hawksbill sea turtle: Implications for beach management and offspring sex ratios. Endangered Species Research, 20, 41–48. https://doi.org/10.3354/esr00489

Kamel, S. J., & Mrosovsky, N. (2005). Repeatability of nesting preferences in the hawksbill sea turtle, Eretmochelys imbricata, and their fitness consequences. Animal Behaviour, 70, 819–828. https://doi.org/10.1016/j.anbehav.2005.01.006

Kamel, S. J., & Mrosovsky, N. (2006a). Deforestation: Risk of sex ratio distortion in hawksbill sea turtles. Ecological Applications, 16, 923–931.

Kamel, S. J., & Mrosovsky, N. (2006b). Inter-seasonal maintenance of individual nest site preferences in hawksbill sea turtles. Ecology, 87, 2947–2952.

King, R., Cheng, W., Tseng, C., Chen, H., & Cheng, I. (2013). Estimating the sex ratio of green sea turtles (Chelonia mydas) in Taiwan by the nest temperature and histological methods. Journal of Experimental Marine Biology and Ecology, 445, 140–147. https://doi.org/10.1016/j.jembe.2013.03.016

Kornaraki, E., Matossian, D. A., Mazaris, A. D., Matsinos, Y. G., & Margaritoulis, D. (2006). Effectiveness of different conservation measures for loggerhead sea turtle (Caretta caretta) nests at Zakynthos Island, Greece. Biological Conservation, 130, 324–330. https://doi.org/10.1016/j.biocon.2005.12.027

Laloë, J., Cozens, J., Renom, B., Taxonera, A., & Hays, G. C. (2017). Climate change and temperature-linked hatching mortality at a globally important sea turtle nesting site. Global Change Biology, https://doi.org/10.1111/gcb.13765.

Laloë, J., Esteban, N., Berkel, J., & Hays, G. C. (2016). Sand temperatures for nesting sea turtles in the Caribbean: Implications for hatching sex ratios in the face of climate change. Journal of Experimental Marine Biology and Ecology, 474, 92–99. https://doi.org/10.1016/j.jembe.2015.09.015

Lewis, T. J., & Wang, K. (1998). Geothermal evidence for deforestation induced warming: Implications for the climatic impact of land development. Geophysical Research Letters, 25, 535–538. https://doi.org/10.1029/98GL00181

Liles, M. J., Altamirano, E., Gadea, V., Chavarria, S., Yañez, I., Melero, D., ... Gaos, A. R. (2016). Community construction through culturally rooted celebration: Turtles all the way down. In A. M. Feldpausch-Parker, H. Bergea, T. R. Peterson, & K. Raitio (Eds.). Environmental communication and community: Constructive and deconstructive dynamics of social transformation (pp. 204–226). London, UK: Routledge.

Liles, M. J., Peterson, M. J., Lincoln, Y. S., Seminoff, J. A., Gaos, A. R., & Peterson, T. R. (2015a). Connecting international conservation priorities with human wellbeing in low-income nations: Lessons from hawksbill turtle conservation in El Salvador. Local Environment, 20, 1383–1404.

Liles, M. J., Peterson, J. M., Seminoff, J. A., Altamirano, E., Henriquez, A. V., Gaos, A. R., ... Peterson, T. R. (2015b). One size does not fit all: Importance of adjusting conservation practices for endangered hawksbill turtles to address local nesting habitat needs in the eastern Pacific Ocean. Biological Conservation, 184, 405–413.

Limpus, C. J. (1980). Observations on the hawksbill turtle (Eretmochelys imbricata) nesting along the Great Barrier Reef. Herpetologica, 36, 265–271.

Limpus, C. (2006). Impacts of climate change on sea turtles: A case study. In: Roundtable on migratory species and climate change. Nairobi, Kenya: CMS COP.

Limpus, C. J., Baker, V., & Miller, J. D. (1979). Movement induced mortality of loggerhead eggs. Herpetologica, 35, 335–338.

Loop, K. A., Miller, J. D., & Limpus, C. J. (1995). Nesting by the hawksbill turtle (Eretmochelys imbricata) on Milman Island, Great Barrier Reef, Australia. Wildlife Research, 22, 241–252.

Lovelock, C. E., Cahoon, D. R., Friess, D. A., Guntenspergen, G. R., Krauss, K. W., Reef, R., ... Triet, T. (2015). The vulnerability of Indo-Pacific mangrove forests to sea-level rise. Nature, 526, 559–563. https://doi.org/10.1038/nature15538

Margrín, G. O., Marenco, J. A., Boulanger, J. P., et al. (2014) Central and South America. In: V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. I. White (Eds.), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (pp. 1499–1566). Cambridge, UK and New York, NY, USA: Cambridge University Press.

Marcovaldi, M. A., Godfrey, M. H., & Mrososky, N. (1997). Estimating sex ratios of loggerhead turtles in Brazil from pivotal incubation durations. Canadian Journal of Zoology-Revue Canadienne De Zoologie, 75, 755–770. https://doi.org/10.1139/z97-097

Marcovaldi, M. A., & Marcovaldi, G. G. (1999). Marine turtles of Brazil: The history and structure of Projecto TAMAR-IBAMA. Biological Conservation, 91, 35–41.

Marcovaldi, M. A. G., Santos, A. J. B., Santos, A. S., Soares, L. S., Lopez, G. G., Godfrey, M. H., ... Fuentes, M. M. P. B. (2014). Spatio-temporal variation in the incubation duration and sex ratio of hawksbill hatchlings: Implication for future management. Journal of Thermal Biology, 44, 70–77. https://doi.org/10.1016/j.jtherbio.2014.06.010

Maulany, R. I., Booth, D. T., & Baxter, G. S. (2012). The effect of incubation temperature on hatching quality in the olive ridley turtle, Lepidochelys olivacea, from Alas Purwo National Park, East Java, Indonesia: Implications for hatchery management. Marine Biology, 159, 2651–2661. https://doi.org/10.1007/s00227-012-2022-6

Morreale, S. J., Ruiz, G. J., Spotila, J. R., & Sundora, E. A. (1982). Temperature-dependent sex determination: Current practices threaten conservation of sea turtles. Science, 216, 1245–1247. https://doi.org/10.1126/science.7079758

Mrososky, N. (2006). Distorting gene pools by conservation: Assessing the case of doomed turtle eggs. Environmental Management, 38, 523–531. https://doi.org/10.1007/s00267-005-0348-2

Mrososky, N., Bass, A., Cornill, L. A., Richardson, J. I., & Richardson, T. H. (1992). Pivotal and beach temperatures for hawksbill turtles nesting in Antigua. Canadian Journal of Zoology, 70, 1920–1925. https://doi.org/10.1139/z92-261

Mrososky, N., Kamel, S. J., Diez, C. E., & Van Dam, R. P. (2009). Methods of estimating natural sex ratios of sea turtles from incubation temperatures and laboratory data. Endangered Species Research, 8, 147–155. https://doi.org/10.3354/esr00200

Mrososky, N., & Pieau, C. (1991). Transitional range of temperature, pivotal temperatures and thermosensitive stages for sex determination in reptiles. Amphibia-Reptilia, 12, 169–179. https://doi.org/10.1163/156853891X00149

Naro-Maciel, E., Mrososky, N., & Marcovaldi, M. A. (1999). Thermal profiles of sea turtle hatcheries and nesting areas at Praia do Forte, Brazil. Chelonian Conservation and Biology, 3, 407–413.

Neeman, N., Robinson, N. J., Paladino, F. V., Spotila, J. R., & O’Connor, M. P. (2015). Phenology shifts in leatherback turtles (Dermochelys coriacea) due to changes in sea surface temperature. Journal of Experimental Marine Biology and Ecology, 462, 113–120. https://doi.org/10.1016/j.jembe.2014.10.019

Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology, 13, 1860–1872. https://doi.org/10.1111/j.1365-2486.2007.01404.x
Patel, S. H., Morreale, S. J., Saba, V. S., Panagopoulou, A., Margaritoulis, D., & Spotila, J. R. (2016). Climate impacts on sea turtle breeding phenology in Greece and associated foraging habitats in the wider Mediterranean region. PLoS ONE, 11, e0157170. https://doi.org/10.1371/journal.pone.0157170

Patino-Martinez, J., Marco, A., Quinones, L., Abella, E., Abad, R. M., & Dieuzé-Uribeondo, J. (2012a). How do hatcheries influence broyonic development of sea turtle eggs? Experimental analysis and isolation of microorganisms in leatherback turtle eggs. Journal of Experimental Zoology, 317A, 47–54.

Patino-Martinez, J., Marco, A., Quinones, L., & Hawkes, L. (2012b). A potential tool to mitigate the impacts of climate change to the caribbean leatherback sea turtle. Global Change Biology, 18, 401–411.

Patricio, A. R., Marques, A., Barbosa, C., Broderick, A. C., Godley, B. J., Hawkes, L. A., ..., Catry, P. (2017). Balanced primary sex ratios and resilience to climate change in a major sea turtle population. Marine Ecology Progress Series, 577, 189–203. https://doi.org/10.3354/meps12242

Pike, D. A. (2013a). Climate influences the global distribution of sea turtle nesting. Global Ecology and Biogeography, 22, 555–566.

Pike, D. A. (2013b). Forecasting range expansion into ecological traps: Climate-mediated shifts in sea turtle nesting beaches and human development. Global Change Biology, 19, 3082–3092.

Pike, D. A. (2014). Forecasting the viability of sea turtle eggs in a warming world. Global Change Biology, 20, 7–15. https://doi.org/10.1111/gcb.12397

Pilcher, N. J., & Enderby, S. (2001). Effects of prolonged retention in hatcheries on green turtle (Chelonia mydas) hatching swimming speed and survival. Journal of Herpetology, 35, 633–638. https://doi.org/10.2307/1565902

Poloczanska, E. S., Limpus, C. J., & Hays, G. C. (2009). Vulnerability of marine turtles to climate change. Advances in Marine Biology, 56, 151–211.

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., ..., Richardson, A. J. (2013). Global imprint of climate change on marine life. Nature Climate Change, 3, 919–925. https://doi.org/10.1038/nclimate1958

Prichard, P. C. (1980). The conservation of sea turtles: Practices and problems. American Zoologist, 20, 609–617. https://doi.org/10.1093/icb/20.3.609

Refsnider, J. M., Bodensteiner, B. L., Reneker, J. L., & Janzen, F. J. (2013). Nest depth may not compensate for sex ratio skew caused by climate change in turtles. Animal Conservation, 16, 481–490. https://doi.org/10.1111/acc.12034

Refsnider, J. M., & Janzen, F. J. (2012). Behavioural plasticity may compensate for climate change in a long-lived reptile with temperature-dependent sex determination. Biological Conservation, 152, 90–95. https://doi.org/10.1016/j.biocon.2012.03.019

República De Nicaragua. (2009). Ley para el desarrollo de las zonas costeras. Ley No. 690, La Gaceta No. 141.

Revuelta, O., León, Y. M., Broderick, A. C., Feliz, P., Godley, B. J., Balbuena, J. A., ..., Tomás, J. (2015). Assessing the efficacy of direct conservation interventions: Clutch protection of the leatherback marine turtle in the Dominican Republic. Oryx, 49, 677–686. https://doi.org/10.1017/S0030060513001488

Rimblot, F., Fretay, J., Mosovsky, N., Lescure, J., & Pieau, C. (1985). Sexual differentiation as a function of the incubation temperature of eggs in the sea turtle Dermochelys coriacea (Vandelli, 1761). Amphibia-Reptilia, 6, 83–92. https://doi.org/10.1163/156853885X00218

Roosenburg, W. M. (1996). Maternal condition and nest site choice: An alternative for the maintenance of environmental sex determination? American Zoologist, 36, 157–168. https://doi.org/10.1093/icb/36.2.157

Saba, V. S., Stock, C. A., Spotila, J. R., Paladinino, F. V., & Santidrián Tomillo, P. (2012). Projected response of an endangered marine turtle population to climate change. Nature Climate Change, 2, 814–820. https://doi.org/10.1038/nclimate1582

Santidrián Tomillo, P., Saba, V. S., Blanco, G. S., Stock, C. A., Paladinino, F. V., & Spotila, J. R. (2012). Climate driven egg and hatching mortality threatens survival of Eastern Pacific leatherback turtles. PLoS ONE, 7, e37602. https://doi.org/10.1371/journal.pone.0037602

Schofield, G., Hobson, V. J., Lillie, M. K. S., Katselidis, K. A., Bishop, C. M., Brown, P., & Hays, G. C. (2010). Inter-annual variability in the home range of breeding turtles: Implications for current and future conservation management. Biological Conservation, 143, 722–730. https://doi.org/10.1016/j.biocon.2009.12.011

Schwanz, L. E., & Janzen, F. J. (2008). Climate change and temperature-dependent sex determination: Can individual plasticity in nesting phenology prevent extreme sex ratios? Physiological and Biochemical Zoology, 81, 826–834. https://doi.org/10.1086/590220

Shefferson, R. P., Mizuta, R., & Hutchings, M. J. (2017). Predicting evolution in response to climate change: The example of sprouting probability in three dormancy-prone orchid species. Royal Society Open Science, 4, 160647. https://doi.org/10.1098/rsos.160647

Sinervo, B., Méndez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiáns, E., Villagrán-Santa Cruz, M., ..., Sites Jr., J. W. (2010). Erosion of lizard diversity by climate change and altered thermal niches. Science, 328, 894–899. https://doi.org/10.1126/science.1184695

Standora, E. A., & Spotila, J. R. (1985). Temperature Dependent Sex Determination in Sea Turtles, Copeia, 711–722.

Telemeaco, R. S., Elphick, M. J., & Shine, R. (2009). Nesting lizards (Bassiana duperreyi) compensate partly, but not completely, for climate change. Ecology, 90, 17–22.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ..., Williams, S. E. (2004). Extinction risk from climate change. Nature, 427, 145–148. https://doi.org/10.1038/nature02121

Valiela, I., Bowen, J. L., & York, J. K. (2001). Mangrove forests: One of the world’s threatened major tropical environments. BioScience, 51, 807–815. https://doi.org/10.1641/0006-3568(2001)051[0807:MFOOTW]2.0.CO;2

Valladares, F., Matessanz, S., Guillhaumon, F., Araújo, M. B., Balaguer, L., Benito-Garzón, M., ..., Zavala, M. A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecology Letters, 17, 1351–1364. https://doi.org/10.1111/ele.12348

Valverde, R. A., Wingard, S., Gómez, F., Tordoit, M. T., & Orrego, C. M. (2010). Field lethal incubation temperature of olive ridley sea turtle Lepidochelys olivacea embryos at a mass nesting rookery. Endangered Species Research, 12, 77–86. https://doi.org/10.3354/esr00296

Van Damme, R., Bauwens, D., Braña, F., & Verheyen, R. F. (1992). Incubation temperature differentially affects hatching time, egg survival, and hatching performance in the lizard Podarcis muralis. Herpetologica, 220–228.

Wallace, B. P., DiMatteo, A. D., Bolten, A. B., Chaloupka, M. Y., Hutchinson, B. J., Abreu-Grobois, F. A., ..., Mast, R. B. (2011). Global conservation priorities for marine turtles. PLoS ONE, 6, e24510. https://doi.org/10.1371/journal.pone.0024510

Weishampel, J. F., Bagley, D. A., & Ehrhart, L. M. (2004). Earlier nesting by loggerhead sea turtles following sea surface warming. Global Change Biology, 10, 1424–1427. https://doi.org/10.1111/j.1529-8817.2003.00817.x

Weishampel, J. F., Bagley, D. A., Ehrhart, L. M., & Weishampel, A. C. (2010). Nesting phenologies of two sympatric sea turtle species related to sea surface temperatures. Endangered Species Research, 12, 41–47. https://doi.org/10.3354/esr00290
Wibbels, T. (2003). Critical approaches to sex determination in sea turtles. In P. L. Lutz, J. A. Musick, & J. Wyneken (Eds.), The biology of sea turtles (pp. 103–134). Boca Raton, FL: CRC Press.

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. Journal of Experimental Marine Biology and Ecology, 451, 105–114. https://doi.org/10.1016/j.jembe.2013.11.005

Woodroffe, C. D., Rogers, K., Mckee, K. L., Lovelock, C. E., Mendelssohn, I. A., & Saintilan, N. (2016). Mangrove sedimentation and response to relative sea-level rise. Annual Review of Marine Science, 8, 243–266. https://doi.org/10.1146/annurev-marine-122414-034025

Yang, L. H., & Rudolf, V. H. W. (2010). Phenology, ontogeny and the effects of climate change on the timing of species interactions. Ecology Letters, 13, 1–10. https://doi.org/10.1111/j.1461-0248.2009.01402.x

Yntema, C. L., & Mrosovsky, N. (1980). Sexual differentiation in hatchling loggerheads (Caretta caretta) incubated at different controlled temperatures. Herpetologica, 36, 33–36.

Zare, R., Vaghefi, M. E., & Kamel, S. J. (2012). Nest location and clutch success of the hawksbill sea turtle (Eretmochelys imbricata) at Shidvar Island, Iran. Chelonia Conservation and Biology, 11, 229–234.