



Trends in abundance and reproductive success of the hawksbill turtle nesting population at Buck Island Reef National Monument, St. Croix, US Virgin Islands

Alexandra G. Gulick^{1,2,*}, Kristen A. Ewen³, Clayton G. Pollock^{3,4}, Zandy M. Hillis-Starr³

¹Scientists in Parks Fellows Program, Ecological Society of America, Washington, DC 20036, USA

²Archie Carr Center for Sea Turtle Research and Department of Biology, University of Florida, Gainesville, Florida 32611, USA

³Division of Resource Management and Research, Buck Island Reef National Monument, National Park Service, St. Croix 00820, US Virgin Islands

⁴Present address: Natural Resource Branch, Dry Tortugas National Park, National Park Service, Key West, Florida 33040, USA

ABSTRACT: Index nesting sites for the Critically Endangered hawksbill turtle *Eretmochelys imbricata* are essential for assessing population trends and demographics, and informing conservation strategies. Using 29 yr (1988–2017) of saturation tagging data from a protected Caribbean index site, we assessed annual trends in abundance and reproductive success for the hawksbill nesting population at Buck Island Reef National Monument (BIRNM), St. Croix, US Virgin Islands. Approximately 43 ± 21 (mean \pm SD) females and 154 ± 60 nests were encountered each year during nocturnal patrols. Remigration interval and inter-nesting period averaged 3.2 ± 1.6 yr and 17.4 ± 7.1 d, respectively. After a significant recovery since 1988, female abundance stabilized during 2007–2017 ($p < 0.01$, $R^2 = 0.82$), whereas nest abundance declined ($p < 0.01$, $R^2 = 0.71$) and neophyte recruitment exhibited a decreasing trend. There was no trend in annual mean hatch success ($69.4 \pm 26.6\%$), emergence success ($63.0 \pm 29.1\%$), and hatchling production (89.2 ± 45.0 individuals clutch⁻¹) during the study period; but clutch size ($p < 0.01$, $R^2 = 0.65$; 142.8 ± 28.9 eggs clutch⁻¹) and female curved carapace length ($p < 0.01$, $R^2 = 0.56$; 88.4 ± 4.7 cm) significantly decreased. The BIRNM population has stabilized, but declines in body size and nest abundance highlight the need for evaluating demographics to diagnose the factor(s) driving changes in abundance and productivity. Our study provides a foundation for evaluating Caribbean hawksbill demographics, while contributing a valuable assessment of clutch size and *in situ* nest success for the species.

KEY WORDS: *Eretmochelys imbricata* · Sea turtles · Index site · Population assessment · Caribbean

1. INTRODUCTION

Hawksbill turtles *Eretmochelys imbricata* are Critically Endangered worldwide, with 85% of index sites having indicated depleted or declining stocks (Meylan 1999, Mortimer & Donnelly 2008). Index sites for monitoring nesting populations, particularly those in protected areas with the capacity to implement long-term saturation tagging programs, are a valuable tool for assessing changes in abundance and population demographics, and informing man-

agement strategies as marine environments continue to be impacted by anthropogenic threats (Ocean Studies Board & National Research Council 2010).

Hawksbill index nesting sites in the Caribbean represent almost half of the current global population of nesting females (Mortimer & Donnelly 2008), with many sites having reported abundance estimates and population trends: Barbados (Beggs et al. 2007); Mona Island, Puerto Rico (van Dam et al. 2013); Guadeloupe (Kamel & Delcroix 2009); Cuba (Moncada et al. 1999); and Jumby Bay, Antigua (Richardson et al. 1999,

*Corresponding author: alexandra.gulick@ufl.edu

2006). The hawksbill nesting population at Buck Island Reef National Monument (BIRNM), St. Croix, US Virgin Islands (USVI) is the primary index nesting beach for hawksbill turtles under US jurisdiction (National Marine Fisheries Service & US Fish and Wildlife Service 1993), and is one of the last major populations to be characterized in the Caribbean region. As a federally protected index site that has implemented long-term monitoring and saturation tagging of hawksbills during the peak nesting season for over 3 decades, BIRNM offers an opportunity to further assess population trends and demographics for this endangered species in the Caribbean.

The National Park Service (NPS) began monitoring sea turtle nesting activity at BIRNM in 1980 in the form of haphazard day patrols conducted by park rangers to document the number of sea turtle tracks and nests (Zullo 1986). Hawksbill populations at BIRNM were extremely low from 1980 to 1985 (max. 22 nests yr⁻¹), with almost all documented nests being predated by invasive mongoose *Herpestes auropunctatus* or poached by humans (Zullo 1986). Following the successful eradication of mongoose from the park by NPS in the early 1990s, predation by invasive rats *Rattus rattus* predominated nest loss, and rats were successfully removed from the park by the mid-1990s. NPS established the Buck Island Sea Turtle Research Program (BISTRP) in 1988 (Phillips & Hillis-Starr 2002), with the goal of using saturation tagging and long-term monitoring to evaluate the status of the hawksbill population in the park.

In this study we used 29 yr (1988–2017) of saturation tagging data collected by the BISTRP to assess temporal trends in annual counts of hawksbill females and nests (hereinafter referred to as abundance), and the following reproductive parameters: hatch success, emergence success, clutch size, hatchling production, and body size (curved carapace length, CCL) of nesting females. This study provides a foundation for evaluating demographic parameters for hawksbill turtles in the Caribbean, outlines management recommendations for this index population, and contributes a valuable assessment of clutch size and the success of *in situ* nests for the species.

2. MATERIALS AND METHODS

2.1. Study site

BIRNM (17.8° N, 64.6° W) is a federal marine protected area managed by the US NPS, located 2.4 km northeast of St. Croix, USVI in the eastern Carib-

bean. The park boundary encompasses an uninhabited island (0.71 km²) and 76.3 km² of submerged marine habitat. The Monument provides critical nesting beach habitat for 4 sea turtle species, but supports mostly hawksbills (Hillis-Starr & Phillips 1998). The island's nesting area extends 1.6 km along the southern shoreline of Buck Island and offers a diversity of habitats conducive to hawksbill nesting (i.e. open beach, seaward vegetation, and beach forest) (Lundgren 2009).

2.2. Data collection and analysis

Each year (1988–2017), NPS staff conducts nocturnal patrols (18:00–06:00 h) of the entire nesting beach for the 12 wk peak nesting season (mid-July to early October), during which 99% of females that deposit nests are encountered and tagged (i.e. saturation tagging). Complete coverage of the beach during nocturnal patrols ensures that all nests, and all females that successfully deposit a nest during the patrol period, are encountered. Because sampling effort can vary by season due to weather events, annual counts of observed females and nests presented in this article are effort-corrected based on female (and nest) encounter rates and the number of patrol nights missed per season (~6 nights).

Each female is assigned a primary tag identification via application of Inconel flipper tags (National Band and Tag Company; Model 1005-681) and Passive Integrated Transponders (Biomark; Model TX1406L). Untagged individuals encountered at BIRNM for the first time receive tags and are classified as first-time nesters (hereinafter referred to as neophytes), although we acknowledge that we could not confirm a female's reproductive status, since laparoscopies were not conducted. Females encountered over successive years are classified as remigrants. Body size, or CCL, of each female is measured from the anterior point of the mid line (nuchal scute) to the posterior tip of the longest supracaudal (Bolten 1999). Additional morphological data and tissue samples for genetic and stable isotope analyses are collected from each nesting female, but these data are not presented in this article. Please refer to Phillips & Hillis-Starr (2002) for more detail on the saturation tagging protocol at BIRNM.

The location of each nest is documented, and nest excavations are conducted at least 72 h after hatchling emergence. The following parameters are determined for each nest, following standard procedures (Phillips

& Hillis-Starr 2002): hatching success (proportion of eggs that hatched), emergence success (the proportion of eggs that produced live hatchlings that reached the beach surface), and clutch size (the total number of eggs in a clutch). Hatchling production (number of live hatchlings produced per clutch) is calculated by multiplying emergence success and clutch size. Nests that were relocated because of close proximity to the tide line are not excluded from the analysis because of the minimal impact of NPS relocation practices on hatch success (see Lundgren 2009). Maximum and minimum values for clutch size were defined by breaks in the frequency distribution for clutch size (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n048p191_supp.pdf; see methods in Bjorndal & Carr 1989), after removing clutches associated with inter-nesting periods of <6 d (Miller 1997). Clutches with ≥ 240 eggs were excluded from our analyses because they represented extreme outliers likely introduced by human error (i.e. 2 neighboring nests counted as a single clutch upon excavation). Clutch sizes with ≤ 61 eggs are excluded from the analysis because 61 eggs is the smallest clutch size repeatedly recorded for individual females — smaller clutch sizes likely represent partial clutches. Extensive data on the location and environmental variables associated with each nest are also collected, but these data are not presented here. Trends in observed and estimated clutch frequency will be reported in a separate manuscript (A. G. Gulick et al. unpubl.). However, it is clear from satellite tagging data collected during inter-nesting periods that some females documented nesting at BIRNM also lay clutches on the nearby, unmonitored beaches of St. Croix during the same nesting season (Iver-son et al. 2016, Hart et al. 2019).

Generalized additive models (GAMs) with negative binomial link functions to account for autocorrelation were used to evaluate temporal (year) effects on annual counts of females and nests (i.e. abundance) during 1988–2017. GAMs with continuous-time first-order autoregressive processes to account for autocorrelation were used to evaluate temporal effects on annual means of the following reproductive parameters: hatch success, emergence success, clutch size, hatchling production, and female body size (CCL). Within-season and within-female variation of reproductive parameters will be evaluated in a separate study (NPS unpubl. data). Models were fit using thin-plate regression splines to evaluate effects

of nonlinear covariates, and smoothness parameters were estimated using REML (Wood 2006). Data were analyzed in R version 4.0.1 (R Core Team 2020) using the 'mgcv' package (Wood 2011). For GAMs that did not yield a significant year effect on the response variable, we present time series point-whisker plots (mean \pm SD) of the response variable.

3. RESULTS

A total of 505 individual females were recorded nesting at BIRNM during 1988–2017, with a mean (\pm SD) of 43 ± 21 females (range, 11–78) and 154 ± 60 nests (range, 79–301) observed each year (Table 1). Female CCL (Fig. 1, Table 1) averaged 88.4 ± 4.7 cm (range, 73.5–113.2 cm). The average remigration interval was 3.2 ± 1.6 yr (median, 3 yr; range, 1–13 yr), and the mean inter-nesting period (Fig. 2) was 17.4 ± 7.1 d (median, 15 d; range, 0–58 d).

Female abundance significantly increased from 1988 to 2007, then somewhat stabilized up to 2017 (Fig. 3A; $p < 0.01$, $R^2 = 0.82$). The number of remigrants and neophytes observed each year was consistent with the overall trend of total female abundance until 2007, but was followed by a declining trend in neophytes from 2007 to 2017 (Figs. 3B & S2). Similarly, nest abundance significantly increased from 1988 to 2007, but exhibited a significant decline during 2007–2017 (Fig. 3C; $p < 0.01$, $R^2 = 0.71$). The low values for female and nest abundance during the year 2000 were an anomaly, and not attributable to changes in monitoring effort

Table 1. Summary statistics for morphological and reproductive parameters of hawksbill turtles *Eretmochelys imbricata* that nested at Buck Island Reef National Monument (1988–2017). See Section 2.2 for how female curved carapace length (CCL) was measured; measurements of individual females encountered in successive years are included. See Section 2.2 and Fig. S1 for justification of minimum and maximum values defined for clutch size (CS). IP: inter-nesting period; HS: hatch success; ES: emergence success; HP: hatchling production

Parameter	N (unit)	Mean \pm SD	Range
Females (n yr ⁻¹)	1293 (observations)	43 \pm 21	11–78
Nests (n yr ⁻¹)	4614 (clutches)	154 \pm 60	79–301
CCL (cm)	2138 (measurements)	88.4 \pm 4.7	73.5–113.2
IP (d)	1349 (annual records)	17.4 \pm 7.1	0–58
HS (%)	2483 (clutches)	69.4 \pm 26.6	0.0–100.0
ES (%)	2479 (clutches)	63.0 \pm 29.1	0.0–100.0
CS (eggs)	2508 (clutches)	142.8 \pm 28.9	62–238
HP (n clutch ⁻¹)	2479 (clutches)	89.2 \pm 45.0	0–226

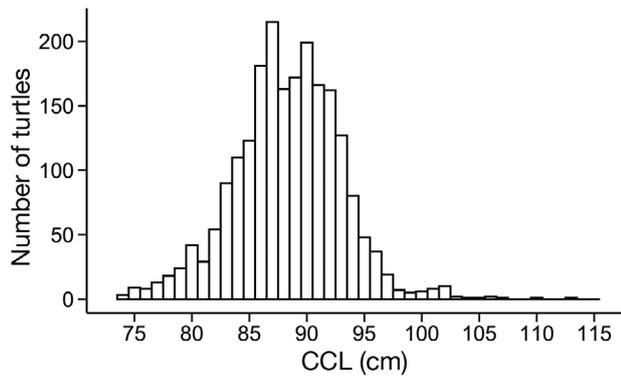


Fig. 1. Size-class frequency distribution of curved carapace length (CCL) of female hawksbill turtles *Eretmochelys imbricata* nesting at Buck Island Reef National Monument over 29 yr (1988–2017) ($n = 2138$; mean \pm SD, 88.4 ± 4.7 cm; range, 73.5–113.2 cm). Measurements of CCL of individual females encountered in successive years were included. See Section 2.2 for how CCL was measured

or weather events that could have impacted nesting beach habitat. Markedly low values for female nest abundance during 2017 were due to the occurrence of 2 category 5 hurricanes that occurred within a 14 d period.

Summary statistics and annual trends for hatch success, hatchling emergence success, clutch size, and hatchling production are reported in Table 1 and Fig. 4. Significant temporal trends were not detected across the 29 yr study period for annual mean hatch success (Fig. 4A; $p = 0.16$, $R^2 = 0.14$), emergence success (Fig. 4B; $p = 0.36$, $R^2 = 0.02$), and hatchling production (Fig. 4D; $p = 0.05$, $R^2 = 0.17$). Hatch success, emergence success, and hatchling production averaged $69.4 \pm 26.6\%$, $63.0 \pm 29.0\%$, and 89.2 ± 45.0 individuals clutch⁻¹ respectively, with lower values recorded during 1995 and 1999 after the occurrence of

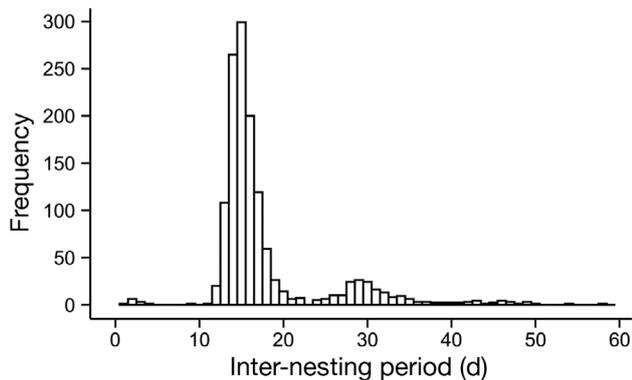


Fig. 2. Frequency distribution of inter-nesting period for hawksbill turtles *Eretmochelys imbricata* that nested at Buck Island Reef National Monument over 29 yr (1988–2017) ($n = 1349$; mean \pm SD, 17.4 ± 7.1 d; range, 0–58 d)

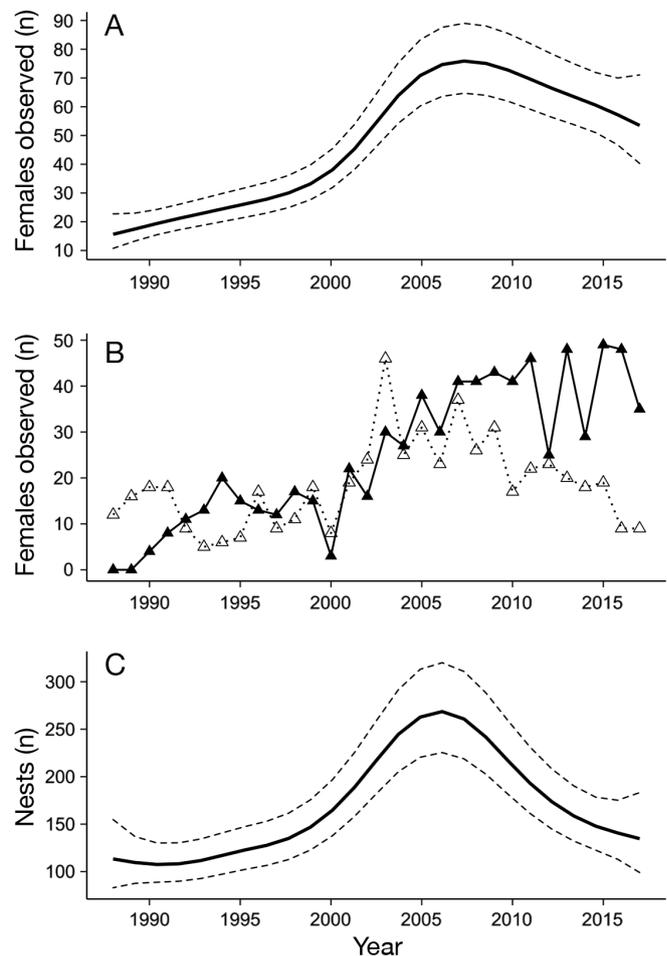


Fig. 3. Effort-adjusted annual counts of female hawksbill turtles *Eretmochelys imbricata* and nests observed at Buck Island Reef National Monument. Saturation tagging was conducted for 29 yr (1988–2017), and all (A) females ($p < 0.01$, $R^2 = 0.82$), (B) including remigrants (\blacktriangle) and neophytes (\triangle), and (C) nests ($p < 0.01$, $R^2 = 0.71$) encountered during nocturnal patrols were counted. Solid lines in A and C: model predictions from generalized additive models with negative binomial link functions; dashed lines: 95% CI

major hurricanes (Fig. 4A,B). Low emergence success and hatchling production during 2015 was due to a temporary sampling protocol change that affected values for that year only. Variation in hatchling production was explained mostly by emergence success (Fig. S3; $p < 0.01$, $R^2 = 0.81$), and not clutch size.

Mean clutch size was 142.8 ± 28.9 eggs, and annual mean clutch size exhibited an overall significant decline across the study period (Fig. 4C; $p < 0.01$, $R^2 = 0.68$). The significant decrease in annual mean clutch size across the study period was partially driven by the significant decline in mean annual CCL of nesting females (Fig. 5; $p < 0.01$, $R^2 = 0.57$).

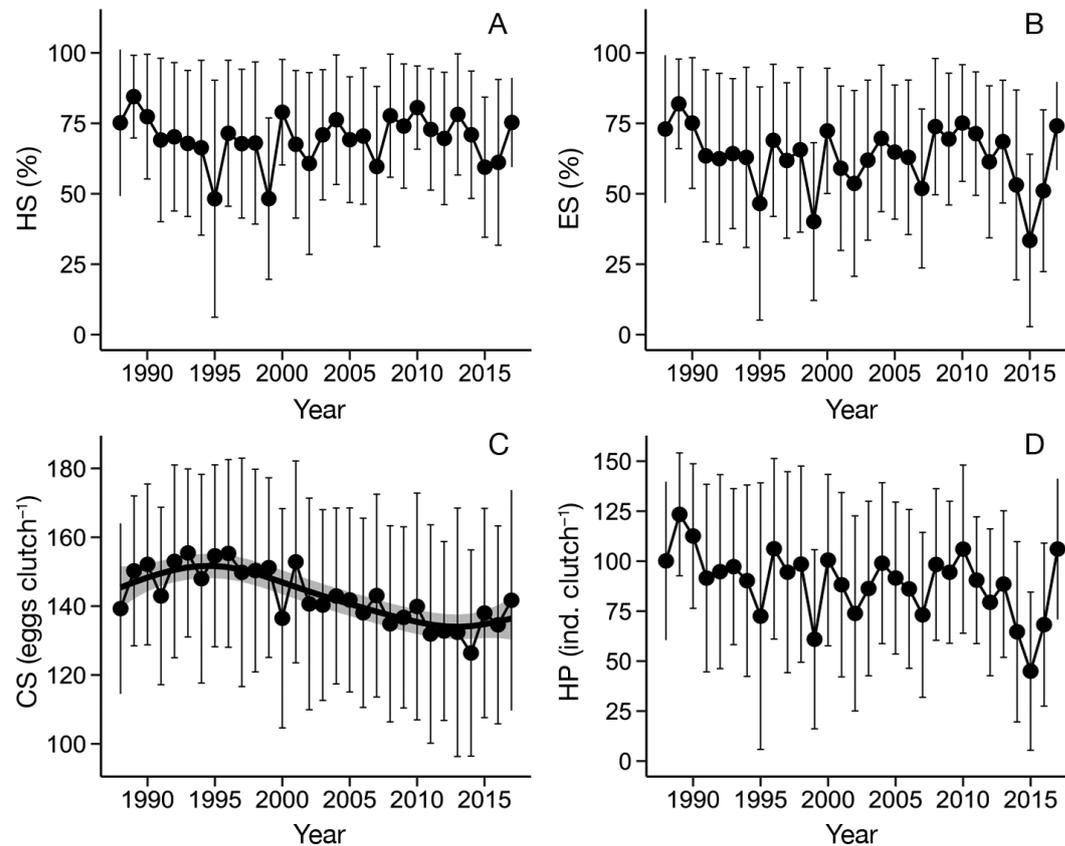


Fig. 4. Graphical summary of reproductive parameters (annual mean \pm SD) for hawksbill turtle (*Eretmochelys imbricata*) nests at Buck Island Reef National Monument (1988–2017): (A) hatching success (HS), (B) hatching emergence success (ES), (C) clutch size (CS), and (D) hatchling production (HP). CS significantly declined during the study period ($p < 0.01$, $R^2 = 0.68$); temporal trends for the other parameters were not significant. Solid trend line in C: predictions from a generalized additive model; shaded area: 95% CI. Major hurricanes that contributed to substantial single-year declines in some reproductive parameters occurred during 1995 and 1999. Low ES and HP during 2015 are due to a protocol change that affected values for that year only

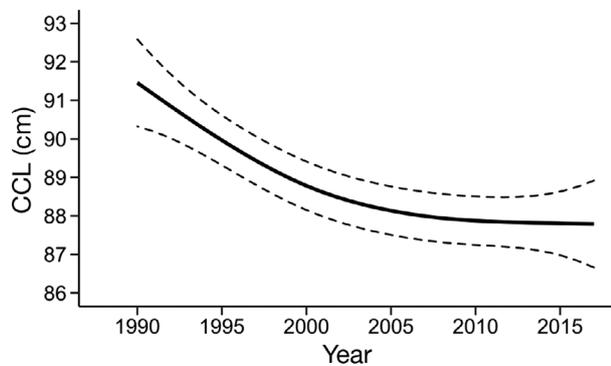


Fig. 5. Curved carapace length (CCL) of female hawksbill turtles *Eretmochelys imbricata* nesting at Buck Island Reef National Monument significantly declined during 1990–2017 ($p < 0.01$, $R^2 = 0.57$). Female CCL measurements obtained during 1988–1989 were excluded from the analysis due to insufficient sample size. Solid trend line: predictions from a generalized additive model; dashed lines: 95% CI. See Section 2.2 for how female CCL was measured

4. DISCUSSION

4.1. Abundance trends and implications for female productivity

The hawksbill nesting population at BIRNM has dramatically increased since the first records of nesting activity in 1980–1985 (Zullo 1986). The initial recovery trend in female abundance from 1988 to 2007 (Fig. 3A) was clearly supported by increased female recruitment to the nesting population (Fig. 3B), resulting in the corresponding increase in nest abundance (Fig. 3C). The rebound of hawksbills at BIRNM is a conservation success attributable to protection under the Endangered Species Act, effective eradication of invasive mammalian predators (mongoose and rats) by 1993 (Hillis-Starr & Phillips 1998, Witmer et al. 2007), increased patrols of park rangers to elimi-

nate poaching, the establishment of long-term monitoring and research efforts via the BISTRP (Hillis-Starr & Phillips 1998), and public education. Although most index nesting sites in the Caribbean have reported declining hawksbill stocks (see Meylan 1999, Mortimer & Donnelly 2008), BIRNM is one of few index sites to report population increases through the mid-2000s, in addition to Antigua (Richardson et al. 2006, Stapleton et al. 2010); Mona Island, Puerto Rico (van Dam et al. 2013); Barbados (Beggs et al. 2007); and Guadeloupe (Kamel & Delcroix 2009).

Following the initial recovery trend from 1988 to 2007, female abundance stabilized during 2007–2017, which was supported mostly by remigrants (Fig. 3B), whereas nest abundance significantly declined (Fig. 3C) and abundance of neophytes exhibited a declining trend after 2007 (Fig. 3B). Although annual mean hatch success, emergence success, and hatchling production did not exhibit temporal trends during 1988–2017 (Fig. 4), significant declines in clutch size (Fig. 4C) and female body size (CCL) (Fig. 5) were detected. These results collectively suggest that nesting habitat-use patterns of females are changing (see Hart et al. 2019), and that female recruitment and productivity may be declining. Several factors could contribute to changes in productivity of this index population, including region-wide ecological regime shifts that degrade hawksbill foraging habitats, to localized changes in shoreline dynamics that impact nesting habitat-use patterns.

Climate change poses a major threat to the survival of sea turtles (Hamann et al. 2013, Rees et al. 2016), and a thorough understanding of population demographics is critical to identifying factors that impact population productivity. Growth dynamics are valuable bio-indicators of environmental change, particularly at regional scales (e.g. Bjorndal et al. 2017). Growth rates of several sea turtle species (Avens et al. 2015, Bjorndal et al. 2017), including hawksbills (Bjorndal et al. 2016, Avens et al. 2021), have significantly declined throughout the Western Atlantic (including the Caribbean) since 1997, a phenomenon likely driven by an ecological regime shift that resulted from the concurrence of long-term ocean warming and the El Niño-Southern Oscillation that occurred in 1997–1998 (the strongest on record) (Bjorndal et al. 2017). Such declines in growth rates could be contributing to the observed decreases in female body size for multiple species across nesting sites in the Western Atlantic (e.g. Phillips et al. 2021), which has important implications for female productivity and hatchling production. It is well documented that clutch size increases with female body size in sea

turtles (e.g. Frazer & Richardson 1986, Broderick et al. 2003, Wallace et al. 2007, Le Gouvello et al. 2020), including hawksbills (Bjorndal et al. 1985). Because clutch size is significantly impacted by the environmental conditions that influence nutritional intake of nesting females (Bjorndal et al. 1985), the long-term annual declines in mean female body size and clutch size observed at BIRNM (Figs. 4C & 5) have important implications for overall hatchling production, and reinforce that an ecological regime shift in the region may be an underlying driver of these declines (Bjorndal et al. 2017). Most of the variation in hatchling production is explained by emergence success (Fig. S3); thereby, any decline in emergence success, combined with reduced clutch size, could affect hatchling production over the long term—particularly as climate change (e.g. sea-level rise, increased storm frequency) impacts nesting beach habitats.

Localized changes to the shoreline dynamics at BIRNM (i.e. beach erosion due to sea-level rise and increased storm frequency) could also be driving changes in nesting habitat use patterns of females. Use of multiple nesting beaches within a single breeding season is a common behavior reported for female hawksbills (e.g. Moncada et al. 1999, Beggs et al. 2007). The decline in nest abundance since 2007 relative to the stability of female abundance (Fig. 3) suggests that this behavior may have become more common in BIRNM hawksbills over the last decade. Satellite tracking studies of female hawksbills nesting at BIRNM have confirmed that some individuals are utilizing beaches in the park and on the neighboring developed island of St. Croix (2.4 km southwest of BIRNM) within a single nesting season (Iverson et al. 2016, Hart et al. 2019). In addition, the number of hawksbill nests observed annually on St. Croix beaches has markedly increased since 2007 (Mortimer & Donnelly 2008), which corresponds to when nest abundance at BIRNM began to decline relative to female abundance. However, it is critical to recognize that the majority of nesting beaches available on St. Croix are unprotected/unmonitored and records of BIRNM females encountered on these beaches are limited, thus providing further justification for the continued value of BIRNM as the primary index nesting beach and saturation tagging program for hawksbills in St. Croix and the USVI. Although multiple factors are likely contributing to ‘spill-over’ of hawksbill nesting activity beyond the park boundary, the recent changes in shoreline dynamics (e.g. erosion, storm berms, and washout of tree roots making the beach inaccessible in key nesting areas) at BIRNM and the corresponding impacts on female

habitat use and availability of nesting habitat warrant further study in order to adapt management strategies.

4.2. Hawksbill recovery plan and management recommendations

The primary goal outlined in the hawksbill recovery plan for the US Caribbean, Gulf of Mexico, and Atlantic is to delist the species if all recovery criteria and actions are met by 2020 (National Marine Fisheries Service & US Fish and Wildlife Service 1993). In the context of nesting populations, such criteria include a statistically significant increase in the annual number of nests over a period of at least 25 yr, and a 75% hatching success rate on major nesting beaches. The recovery plan requires that these criteria be met at BIRNM and Mona Island, Puerto Rico (the primary index nesting sites under US jurisdiction) for the species to be delisted.

Based on the trends in abundance and reproductive parameters presented in this study, BIRNM is at a critical point where the female population appears to have stabilized, while annual hatching success has been maintained at $69.4 \pm 26.6\%$. However, declines in female body size and clutch size (this study), decades of female-biased sex ratios of BIRNM hatchlings (Wibbels et al. 1999, Lyons 2020), and regional declines in hawksbill growth rates (Bjorndal et al. 2016) warrant concern. Therefore, it is unclear whether the observed trends in abundance and reproductive success reflect those of a healthy, aging female population or are early signs of severe decline that warrant management intervention. Although the hawksbill population at BIRNM has rebounded dramatically and some of the recovery criteria are close to being met in the park, some factors likely driving changes in abundance and reproductive success were not anticipated when the recovery plan was drafted in the early 1990s (i.e. sea-level rise, increasing storm strength and frequency, increasing temperatures, beach erosion etc.). At that time, the main focus of the recovery plan was to reduce illegal take by humans and establish long-term protected index sites for the species (National Marine Fisheries Service & US Fish and Wildlife Service 1993), and many adjacent unprotected and unmonitored nesting sites were excluded due to lack of data (Mortimer & Donnelly 2008).

Our results highlight the value of BIRNM as an index nesting site for assessing hawksbill status and guiding species recovery plans, further emphasizing

the need for continued investment in the saturation tagging program at BIRNM to protect this index population. Our study provides a foundation for assessments of female population demographics (including changes to clutch frequency [A. G. Gulick et al. unpubl.], senescence, etc.), which will be essential to determining the drivers of changes in abundance and reproductive parameters, and informing management action for this species in the Caribbean.

Acknowledgements. Funding for the Buck Island Sea Turtle Research Program (BISTRP) was provided by the National Park Service (NPS) at Buck Island Reef National Monument in St. Croix, US Virgin Islands. Research was conducted under US Fish and Wildlife Service Permit #TE38906B-0. We thank Joel A. Tutein, Brendalee Phillips, Ian Lundgren, and the many NPS biologists, technicians, interns, and volunteers for their significant contributions to the BISTRP. We appreciate Ms. Elizabeth Armstrong and staff of the Buccaneer Hotel and Resort for hosting decades of seasonal interns and for supporting BISTRP education and outreach efforts. Support for the corresponding author A.G.G. during the drafting of this manuscript was provided by a Scientists in Parks Fellowship through the Ecological Society of America and NPS. We thank Karen Bjorndal for providing feedback on earlier versions of the manuscript.

LITERATURE CITED

- ✦ Avens L, Goshe LR, Coggins L, Snover ML, Pajuelo M, Bjorndal KA, Bolten AB (2015) Age and size at maturation- and adult-stage duration for loggerhead sea turtles in the western North Atlantic. *Mar Biol* 162:1749–1767
- ✦ Avens L, Ramirez MD, Goshe LR, Clark JM and others (2021) Hawksbill sea turtle life-stage durations, somatic growth patterns, and age at maturation. *Endang Species Res* 45:127–145
- ✦ Beggs J, Horrocks J, Krueger B (2007) Increase in hawksbill sea turtle *Eretmochelys imbricata* nesting in Barbados, West Indies. *Endang Species Res* 3:159–168
- Bjorndal KA, Carr A (1989) Variation in clutch size and egg size in the green turtle nesting population at Tortuguero, Costa Rica. *Herpetologica* 45:181–189
- ✦ Bjorndal KA, Carr A, Meylan AB, Mortimer JA (1985) Reproductive biology of the hawksbill *Eretmochelys imbricata* at Tortuguero, Costa Rica, with notes on the ecology of the species in the Caribbean. *Biol Conserv* 34: 353–368
- ✦ Bjorndal KA, Chaloupka M, Saba VS, Diez CE and others (2016) Somatic growth dynamics of West Atlantic hawksbill sea turtles: a spatio-temporal perspective. *Ecosphere* 7:1–14
- ✦ Bjorndal KA, Bolten AB, Chaloupka M, Saba VS and others (2017) Ecological regime shift drives declining growth rates of sea turtles throughout the West Atlantic. *Glob Change Biol* 23:4556–4568
- Bolten AB (1999) Techniques for measuring sea turtles. In: Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds) *Research and management techniques for the conservation of sea turtles*. IUCN/SSC Marine Turtle Specialist Group, Washington, DC, p 1–5

- Broderick AC, Glen F, Godley BJ, Hays GC (2003) Variation in reproductive output of marine turtles. *J Exp Mar Biol Ecol* 288:95–109
- Frazer NB, Richardson JI (1986) The relationship of clutch size and frequency to body size in loggerhead turtles, *Caretta caretta*. *J Herpetol* 20:81–84
- Hamann M, Fuentes MMPB, Ban NC, Mocellin VJL (2013) Climate change and marine turtles. In: Wyneken J, Lohmann KJ, Musick JA (eds) *The biology of sea turtles*. CRC Press, Boca Raton, FL, p 353–378
- Hart KM, Iverson AR, Benschoter AM, Fujisaki I and others (2019) Satellite tracking of hawksbill turtles nesting at Buck Island Reef National Monument, US Virgin Islands: inter-nesting and foraging period movements and migrations. *Biol Conserv* 229:1–13
- Hillis-Starr ZM, Phillips B (1998) Buck Island Reef National Monument hawksbill nesting beach study— Could conservation be working? In: *Proc 18th Int Sea Turtle Symp*. NOAA Tech Memo MFS-SEFSC-436, p 11–14
- Iverson A, Hart K, Fujisaki I (2016) Hawksbill satellite-tracking case study: implications for remigration interval and population estimates. *Mar Turtle Newsl* 148:2–7
- Kamel SJ, Delcroix E (2009) Nesting ecology of the hawksbill turtle, *Eretmochelys imbricata*, in Guadeloupe, French West Indies from 2000–07. *J Herpetol* 43:367–376
- Le Gouvello DZM, Nel R, Cloete AE (2020) The influence of individual size on clutch size and hatchling fitness traits in sea turtles. *J Exp Mar Biol Ecol* 527:151372
- Lundgren I (2009) Relation of abiotic conditions to hatch success for relocated hawksbill sea turtle, *Eretmochelys imbricata*, nests at Buck Island, St. Croix, US Virgin Islands. MS thesis, University of the Virgin Islands, St. Thomas
- Lyons E (2020) How egg size, incubation temperatures, and hatch success relate within a population of hawksbill sea turtles. MS thesis, University of Miami
- Meylan A (1999) Status of the hawksbill turtle (*Eretmochelys imbricata*) in the Caribbean region. *Chelonian Conserv Biol* 3:177–184
- Miller JD (1997) Reproduction in sea turtles. In: Lutz PL, Musick JA (eds) *Biology of sea turtles*, Vol I. CRC Press, Boca Raton, FL, p 51–81
- Moncada F, Carrillo E, Saenz A, Nodarse G (1999) Reproduction and nesting of the hawksbill turtle, *Eretmochelys imbricata*, in the Cuban archipelago. *Chelonian Conserv Biol* 3:257–263
- Mortimer JA, Donnelly M (2008) *Eretmochelys imbricata*. IUCN Red List of Threatened Species 2008: e.T8005A12881238
- National Marine Fisheries Service, US Fish and Wildlife Service (1993) Recovery plan for hawksbill turtles in the U.S. Caribbean Sea, Atlantic Ocean, and Gulf of Mexico. National Marine Fisheries Service, St. Petersburg, FL
- Ocean Studies Board, National Research Council (2010) Assessment of sea-turtle status and trends: integrating demography and abundance. National Academies Press, Washington, DC
- Phillips B, Hillis-Starr ZM (2002) Sea turtle nesting research & monitoring protocol. US Geological Survey, St. John, US Virgin Islands
- Phillips KF, Stahelin GD, Chabot RM, Mansfield KL (2021) Long-term trends in marine turtle size at maturity at an important Atlantic rookery. *Ecosphere* 12:e03631
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org
- Rees AF, Alfaro-Shigueto J, Barata PCR, Bjorndal KA and others (2016) Are we working towards global research priorities for management and conservation of sea turtles? *Endang Species Res* 31:337–382
- Richardson JI, Bell R, Richardson TH (1999) Population ecology and demographic implications drawn from an 11-year study of nesting hawksbill, *Eretmochelys imbricata*, at Jumby Bay, Long Island, Antigua, West Indies. *Chelonian Conserv Biol* 3:244–250
- Richardson JI, Bell R, Mason PA, Andrews KM, Bjorkland R, Cai Y, Bell R (2006) Eighteen years of saturation tagging data reveal a significant increase in nesting hawksbill sea turtles (*Eretmochelys imbricata*) on Long Island, Antigua. *Anim Conserv* 9:302–307
- Stapleton S, Tilley D, Levasseur K (2010) Monitoring Antigua's hawksbills (*Eretmochelys imbricata*): a population update from more than two decades of saturation tagging at Jumby Bay. *Mar Turtle Newsl* 127:19–22
- van Dam RP, Diez CE, Munoz KGB, Gallego CR (2013) Ongoing recovery of the hawksbill turtle population breeding at Mona Island, Puerto Rico. In: *Proc 33rd Annu Symp Sea Turtle Biol Conserv*. NOAA Tech Memo NMFS-SEFSC-645, p 204
- Wallace BP, Sotherland PR, Tomillo PS, Reina RD, Spotila JR, Paladino FV (2007) Maternal investment in reproduction and its consequences in leatherback turtles. *Oecologia* 152:37–47
- Wibbels T, Hillis-Starr ZM, Phillips B (1999) Female-biased sex ratios of hatchling hawksbill sea turtles from a Caribbean nesting beach. *J Herpetol* 33:142–144
- Witmer GW, Boyd F, Hillis-Starr Z (2007) The successful eradication of introduced roof rats (*Rattus rattus*) from Buck Island using diphacinone, followed by an irruption of house mice (*Mus musculus*). *Wildl Res* 34:108–115
- Wood S (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC, Boca Raton, FL
- Wood S (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc B* 73:3–36
- Zullo ES (1986) Sea turtle nesting at Virgin Island National Park and Buck Island Reef National Monument 1980–1985. National Parks Service Final Report. US NPS, St John, US Virgin Islands

Editorial responsibility: Clive McMahon,
Hobart, Tasmania, Australia
Reviewed by: 2 anonymous referees

Submitted: December 22, 2021
Accepted: May 6, 2022
Proofs received from author(s): July 20, 2022