

ARTICLE

Coastal and Marine Ecology

Long-term apparent survival of a cold-stunned subpopulation of juvenile green turtles

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Abstract

Understanding the effects of extreme weather on animal populations is fundamental to ecological and conservation sciences and species management. Climate change has resulted in both warm and cold temperature extremes, including an increased frequency of severe cold snaps at middle latitudes in North America. These unusually cold air masses cause rapid declines in near-shore ocean temperatures in coastal areas, with detrimental effects on marine organisms. Acute cold-stun events (hereafter cold stuns) occur when hundreds to thousands of resident juvenile sea turtles fail to escape shallow water during cold snaps. Human intervention through rescue and recovery largely mitigates direct juvenile sea turtle mortality, but delayed effects of cold stuns on rescued individuals are not well understood. Our objective was to examine long-term juvenile green turtle (*Chelonia mydas*) survival across four cold stuns of varying severity in St. Joseph Bay, Florida, between 2010 and 2018. We used the classic Cormack–Jolly–Seber model in a hierarchical Bayesian framework to estimate apparent survival (i.e., emigration and mortality) of rescued turtles at different time intervals. Our results indicated about half of a cohort rescued during a severe cold stun in January 2010 likely remained in the population 1 year later, with 10%–20% remaining 4 years later, and as few as 5% by 2018. The results also suggested higher apparent survival for cohorts rescued during two subsequent milder cold stuns. Emigration was a more plausible ecological explanation for low apparent survival than delayed mortality. Potential ecological mechanisms underlying emigration include a reduction in food availability and a behavioral response to either the severe weather event or handling during rescue (or both). However, the typical annual turnover of juvenile green turtles, though assumed low, is not well known in St. Joseph Bay. Thus, our apparent survival estimates may be reflective of higher-than-expected emigration in the broader population. Our study provides important baseline information about long-term juvenile sea turtle survival after cold stuns in temperate regions. We also highlight the importance of strategic monitoring between cold stuns to examine additional ecological questions.

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KEYWORDS

Bayesian framework, Cormack–Jolly–Seber model, extreme weather events, juvenile sea turtles

INTRODUCTION

Extreme weather (e.g., flooding, droughts, and temperature extremes) is a natural regulator of animal populations (Moreno & Møller, 2011; Parmesan et al., 2000; Solomon, 1949). Understanding the effects of extreme weather on survival, abundance, and demographics is fundamental to ecological and conservation sciences and population management. However, population responses to extreme weather, particularly across different levels of severity, are inherently difficult to study. Extreme weather events are, by nature, hard to predict, making study design and logistics challenging. There is also a temporal mismatch between the timing and duration of the event and population responses (Anderson et al., 2017; Gill, 2015; Jentsch et al., 2007). Short-term survival after extreme weather events is sometimes possible to document, but longer term effects on populations are often unknown (Lamont et al., 2018; Neilson et al., 2020).

Climate change has altered global weather patterns, resulting in continued increases in the frequency and magnitude of extreme events (Anderson et al., 2017; Tippet, 2018; Zhang et al., 2018). The global long-term trend of increasingly warmer temperatures has motivated numerous assessments of animal population responses to heatwaves (e.g., Alfonso et al., 2021; Davies et al., 2013; Gálvez et al., 2020; Kruuk et al., 2015; Vinagre et al., 2018). However, climate change has also caused abnormally cold weather in some regions, and ecological consequences are relatively understudied. For example, there has been an increase in severe winter cold snaps in temperate areas of middle latitudes in the Northern Hemisphere (Iida et al., 2020; Latimer & Zuckerberg, 2019; Xie & Zhang, 2017). In coastal areas, these unusually cold air masses cause rapid drops in nearshore ocean temperatures. Extreme temperature declines in shallow waters can be detrimental to marine organisms (e.g., Colella et al., 2012; Roberts et al., 1982; Szekeres et al., 2016), but identifying population-level effects has been limited to few taxa.

Sea turtles are among the most susceptible marine taxa to colder water temperatures. Hypothermia resulting from exposure to water temperatures below 10°C (hereafter cold stunning) can lead to severe lethargy and stranding (i.e., floating or washed ashore; Innis et al., 2007; Morreale et al., 1992; Witherington & Ehrhart, 1989). Chronic cold stunning associated with prolonged suboptimal water temperatures commonly affects seasonal residents

in temperate regions (Foley et al., 2007). However, acute cold-stun events (hereafter cold stuns) are rare and occur when hundreds to thousands of juvenile sea turtles fail to escape shallow water during an abrupt cold snap (Foley et al., 2007; Griffin et al., 2019; Roberts et al., 2014). Juvenile sea turtles are more susceptible to cold stuns than adults due to their affinity for shallow, nearshore foraging habitats in bays (Bolten et al., 2002; Roberts et al., 2014). Cold stuns are historically most common in the northern Gulf of Mexico and Atlantic Ocean (Witherington & Ehrhart, 1989), with increased occurrence in recent decades (Griffin et al., 2019; Still et al., 2005). Juvenile sea turtles are also expanding their northern ranges (Griffin et al., 2019; Osland et al., 2021), making them more likely to encounter cold snaps and associated water temperature declines. All sea turtle species are of conservation concern globally (Ceriani et al., 2019). Sea turtles have low survivorship (Heppell et al., 2002); thus, high juvenile survival is critical to long-term population recovery and persistence (Congdon et al., 1993; Crouse et al., 1987).

Human intervention through rescue and recovery can largely mitigate direct juvenile sea turtle mortality from cold stuns, but delayed effects on rescued individuals are not well understood. Cold-stun mortalities are presumed high without intervention, and death is a near certainty for juveniles exposed to water temperatures <6°C for prolonged periods (Roberts et al., 2014; Schwartz, 1978; Still et al., 2005). Dead recoveries also indicate low survival once stranded (Avens et al., 2012; Gerle et al., 2000; Shaver et al., 2017). Sea turtle rescue efforts are common during cold stuns and reduce direct mortalities by ~80% (Foley et al., 2007; McMichael et al., 2008; Shaver et al., 2017). Even with rehabilitation, delayed responses (e.g., mortality, reduced fitness, and altered behavior) may occur due to physiological and physical effects of cold stunning. For example, cold stunning can cause severe electrolyte imbalances (Innis, Ravich, et al., 2009; Stacy et al., 2013), impair respiratory and metabolic function (Innis et al., 2007; Keller et al., 2012), and lead to secondary infections (Manire et al., 2002; Williams et al., 2012). Severe eye (Foley et al., 2007; Lively et al., 2019) and shell damage (Foley et al., 2007; Innis, Nyaoke, et al., 2009) can also occur due to inability to swim, infection, and vulnerability to predators. In addition, cold stunning can elevate stress hormones (Hunt et al., 2012), potentially leading to prolonged changes in movement and foraging patterns. Some studies have documented delayed responses of

rescued cold-stunned sea turtles (e.g., McMichael et al., 2006, 2008; Shaver et al., 2017); however, research has been limited to <4 years and <100 individuals.

Our objective was to examine the long-term juvenile green turtle (*Chelonia mydas*) apparent survival across four cold stuns of varying severity in St. Joseph Bay, Florida (FL), between 2010 and 2018. Juvenile green turtles are considered year-round and multiyear residents of St. Joseph Bay (Avens et al., 2012; Foley et al., 2007; Lamont et al., 2015), thus making them the most susceptible sea turtle species to cold stunning. Juvenile green turtles exhibit strong site fidelity to neritic foraging areas in bays (e.g., Bass et al., 2006; Redfoot & Ehrhart, 2013; Shimada et al., 2014). Although studies are limited, satellite tracking (Lamont et al., 2018), telemetry (Lamont et al., 2015), and tag recoveries (Lamont & Johnson, 2021) support this hypothesis of high fidelity of juvenile green turtles to St. Joseph Bay. All green turtle populations in the United States are federally listed, with Florida populations considered threatened (National Marine Fisheries Service & U.S. Fish and Wildlife Service, 2016). Although the primary goal of cold-stun response teams was sea turtle rescue, mark–recapture data were collected in a fashion appropriate for basic survival modeling (see *Cold-stun mark and recapture data* in *Methods*). Mark–recapture studies for sea turtles are often constrained by poor sampling efficiency (Epperly et al., 2007; Heithaus et al., 2005; Heppell et al., 2003). Cold stuns provide a unique opportunity to mark a large number of turtles and improve return rates of previously marked individuals. We estimated juvenile green turtle survival using the classic Cormack–Jolly–Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965), which allows for a single encounter in each capture occasion (see *Survival modeling* in *Methods*). We are not aware of any studies that have examined apparent survival for rescued cold-stun sea turtles using a large number of individuals (i.e., >1000) across multiple events (but see Innis et al., 2019, for summaries of reencounters of rehabilitated cold-stunned sea turtles). Our study provides essential baseline ecological information that supports future cold-stun studies and long-term sea turtle conservation in both the northern Gulf of Mexico and other temperate regions. Our modeling approach can be extended to other survey designs that address additional ecological questions.

METHODS

Study area

St. Joseph Bay (~26,000 ha) is located in the northern Gulf of Mexico off the coast of northwest FL (Figure 1).

Shallow, nearshore habitats are primarily oyster reef or salt marsh, with annual seagrass common in clear-water areas (Withers & Tunnell, 2007). Seagrass beds in shallow areas of St. Joseph Bay are primarily composed of turtlegrass, *Thalassia testudinum* (Valentine et al., 1994). The substrate in St. Joseph Bay is predominately fine to medium sand and with some silt and clay. In contrast to tropical waters of the southern portion, the northern Gulf of Mexico is considered temperate with colder and more variable water temperatures during the winter (Withers & Tunnell, 2007). Shallow areas in St. Joseph Bay are often clear, with high turbidity in deeper waters (Valentine et al., 1994).

The St. Joseph Bay sea turtle assemblage is primarily composed of green turtles, though Kemp's ridleys (*Lepidochelys kempii*) and loggerheads (*Caretta caretta*) also occur (Lamont & Iverson, 2018). Juvenile green turtles not only are primary herbivores but may also feed on invertebrates (Bugoni et al., 2003; Mortimer, 1981; Nagaoka et al., 2012). Green turtles undertake several shifts in habitat use throughout their lives including an oceanic-to-neritic shift as juveniles (Reich et al., 2007). At or near sexual maturity, green turtles migrate to adult foraging grounds (Bjorndal et al., 2005). Size at sexual maturity varies across regions with East Pacific green turtles maturing at smaller sizes than northwest Atlantic green turtles (Avens & Snover, 2013; Seminoff, Resendiz, Nichols, & Jones, 2002). Body size information indicates green turtles in St. Joseph Bay emigrate before reaching ~80 cm straight carapace length (Avens et al., 2012; Lamont & Johnson, 2021). St. Joseph Bay is highly susceptible to rapid water temperature declines due to its topography and location (Foley et al., 2007). Some of the largest cold stuns in the US history have occurred in St. Joseph Bay, with >1000 stranded juvenile green turtles documented in both January 2010 and 2018 (Avens et al., 2012; Lamont et al., 2018).

Cold-stun mark and recapture data

For purposes of the study, we defined a cold stun as a rapid nearshore water temperature decline causing ≥ 100 juvenile green turtles to wash ashore. The data encompassed more severe cold stuns (>1000 turtles) from 7 to 14 January 2010 and from 14 to 21 January 2018 (hereafter occasion 1 and occasion 4) and less severe cold stuns (100–200 turtles) from 13 to 15 January 2011 and from 7 to 9 January 2014 (hereafter occasion 2 and occasion 3; Table 1). We only considered recaptures during occasion 4 for modeling purposes because newly encountered individuals do not provide information about survival (Kéry & Schaub, 2012; Lebreton et al., 1992).

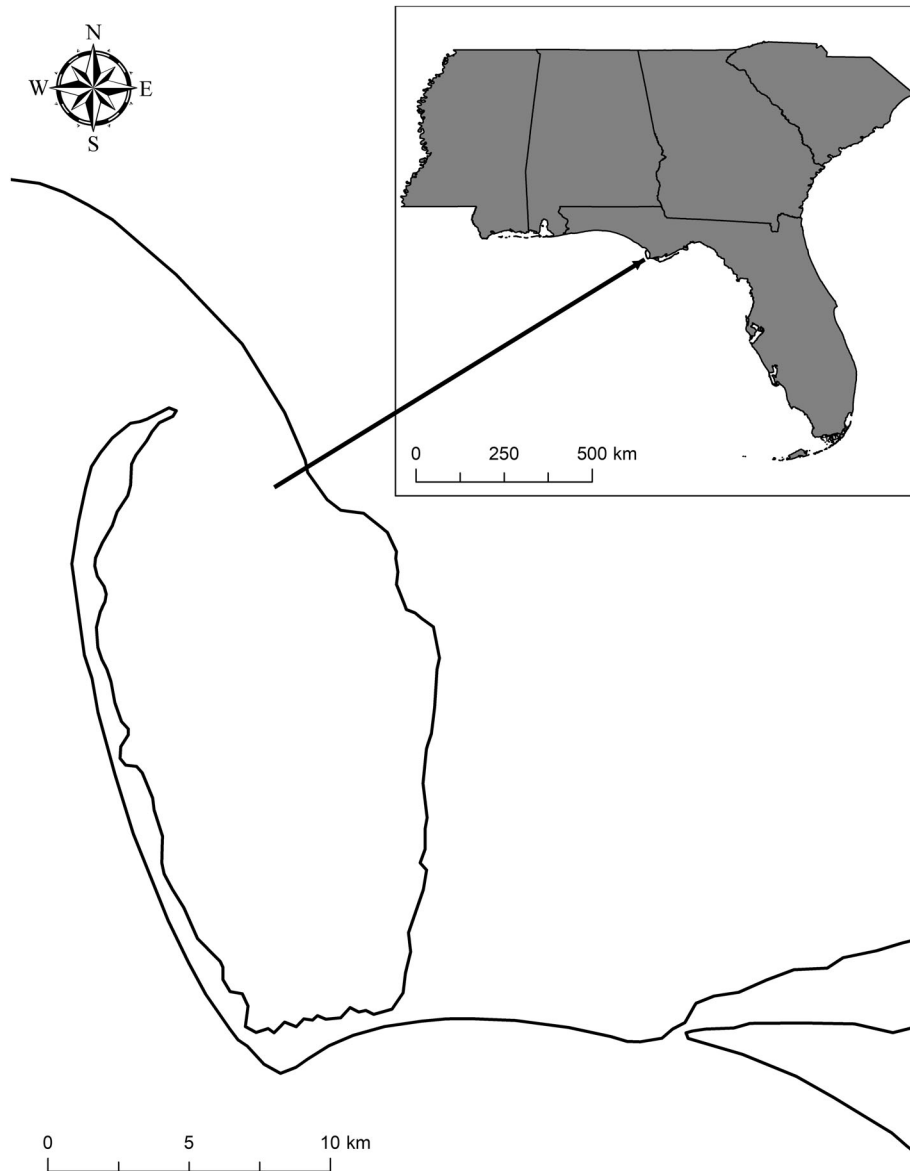


FIGURE 1 Map of St. Joseph Bay, FL, in the northern Gulf of Mexico.

TABLE 1 Summary of marked ($n = 1487$) and recaptured ($n = 171$) juvenile green sea turtles across occasions 1–4 with straight carapace length (mean \pm SD).

Occasion (t)	No. marked	Carapace length (cm)	Turtles/h	No. recaptured ($t = 2$)	No. recaptured ($t = 3$)	No. recaptured ($t = 4$)
One	1183	38.97 \pm 10.27	24.65	119	18	6
Two	182	34.67 \pm 8.12	10.11	NA	2	8
Three	122	37.34 \pm 8.62	6.78	NA	NA	18
Four	NA		24.19	NA	NA	NA

Note: Turtles/h approximates catch rates using an average of 6 h/day of surveying. Only recaptured turtles were considered for occasion 4.

We primarily used juvenile green turtle mark–recapture data compiled during cold stuns for the Florida Fish and Wildlife Conservation Commission (FWC). Intensive surveys to identify cold-stunned turtles were performed on foot, boat, and kayak. The surveys were conducted

primarily in the southwest portion of St. Joseph Bay (~30% of the bay) because prevailing winter winds push cold-stunned turtles in this direction (Roberts et al., 2014). The surveys were performed with a similar effort in all portions of the area. The size of the survey crew and daily

effort varied within and among occasions, ranging from 10 to 100 persons/day and from 4 to 8 h/day, respectively. The crew primarily comprised US Geological Survey (USGS) biologists, along with FWC and US Fish and Wildlife Service scientists and volunteers from the general public. The number of marked turtles and catch rates were reflective of the severity of the cold stun, with the vast majority of turtles marked during occasion 1.

Rescued juvenile turtles were transported to rehabilitation facilities at Gulf World Marine Park in Panama City Beach, FL. Turtles were placed in warm tanks with 15–20°C water and monitored by a veterinarian. Most turtles did not require additional treatment and were not fed in captivity. Rehabilitated turtles were measured and marked with a passive integrated transponder tag subcutaneously in the left front flipper. Marking was done only by experienced turtle biologists. Passive integrated transponder tags have high retention in long-term sea turtle mark–recapture studies (Omeyer et al., 2019). Most (>95%) rescued juvenile green turtles recovered within 2 weeks. Successful recovery was determined by a veterinarian’s health assessment. Turtles were released either in the outer portion of St. Joseph Bay or in the adjacent waters of the Gulf of Mexico to avoid additional exposure to cold temperatures.

We supplemented cold-stun data in occasions 2, 3, and 4 to improve return rates using USGS sampling in St. Joseph Bay between cold stuns (i.e., the open periods). The USGS data are better described as resightings (or relocations) with periodic sampling from late spring to early winter each year. The sampling targeted seagrass habitats in the shallower southern portion of the bay to increase capture efficiency. Green turtles have been shown to have a high affinity for this area of St. Joseph Bay from spring through fall with daily movements (Lamont et al., 2015; Lamont & Iverson, 2018). Thus, it was reasonable to assume an equal chance of capture for each turtle that was present. Boat sampling was conducted by surveying habitat <4 m deep using a variety of methods (i.e., dip-, strike-, and cast-netting, and hand capture). Set nets were also haphazardly deployed in the same area of the bay. It was not possible to use a joint-data model design to fully incorporate the USGS resightings because of a low number of recaptures (also see *Conservation implications* in *Discussion*). However, these data provided important information about survival (i.e., evidence that a turtle survived to the next cold stun), and we only used resightings in late September to late December prior to the cold stun ($n = 12$). We also allowed recapture probability to vary by occasion (see *Survival modeling*) to allow for a nonconstant effect on model estimates. The inclusion of the resightings did expand the beginning of the closed period. However, this additional time was not appreciable for interpreting

apparent survival given the long open periods between cold stuns. Also, the CJS model is robust to the assumption of equal capture intervals among individuals (Hargrove & Borland, 1994).

Recaptures during occasions 2–4 allowed us to examine survival at 1-, 4-, and 8-year intervals for a large cohort of rescued cold-stunned green turtles. The unbalanced sample size primarily limits inference to turtles marked in occasion 1. However, turtles marked in occasions 2 and 3 provided some information on survival in milder cold stuns and contributed to overall return rates. It was not reasonable to assume marked turtles represented either cold-stunned turtles that were not rescued or the broader St. Joseph Bay population (see *Discussion*). Thus, inference about survival can only be extended to any unmarked rescued turtles (<5% of those rescued).

Survival modeling

The CJS model is fundamentally a hierarchical model that distinguishes between a binary latent state (“alive” or “dead”) and a binary observed state (captured or not captured; Kéry & Schaub, 2012; Lebreton et al., 1992). Observed capture history data y_{it} are recorded as 1 if individual i is captured at occasion t and zero if not captured. In the CJS model, y_{it} are expressed in terms of a latent variable z_{it} ($z_{it} = 1$ if alive, $z_{it} = 0$ if dead) and the parameters apparent survival probability ϕ (the probability of remaining in the population at $t + 1$) and recapture probability p (the probability of recapturing a remaining marked individual at t). We emphasize that here p is reflective of the efficiency of capturing remaining marked juvenile green turtles during a cold stun and not a measure of the proportion of cold-stunned turtles rescued. The inclusion of z ensures latent-state transitions are constrained to alive to dead (i.e., emigration is permanent and no zombies). Unlike the similar Jolly–Seber model (Jolly, 1965; Seber, 1965), the CJS model fixes the initial latent state of each individual at one and does not model the initial capture process (i.e., it conditions on the first capture). The CJS model assumes occasions are instantaneous (i.e., a snapshot), with no closure assumption between occasions. The latent process is described as follows:

$$z_{i,f} = 1,$$

$$z_{it+1} | z_{it} \sim \text{Bernoulli}(z_{it}\phi),$$

where f is a vector of marking occasions. The observation process is described as follows:

$$y_{it} | z_{it} \sim \text{Bernoulli}(z_{it}p).$$

We used the fully time-dependent formulation of the CJS model (i.e., $\phi(t)$, $p(t)$; Cooch & White, 2021) to allow estimates of ϕ and p to vary among occasions. We treated occasion as random, which modeled occasions as a trade-off between individual fit and the constraint of the group mean hyperparameter (i.e., estimates shrink toward the central tendency). Estimates are computationally similar using either a fixed or a random approach with few levels of a factor (i.e., shrinkage is minimal). However, treating occasion as random in a CJS model eliminates the identifiability problem when estimating the last period for ϕ and p (Brooks et al., 2000; Kéry & Schaub, 2012). Also, with >2 levels of the occasion factor, some degree of robustness was achieved by treating it as random versus fixed (Gelman & Hill, 2007; Wagner et al., 2006). We estimated both ϕ and p as a linear function of the covariate notch-to-notch straight carapace length at marking (hereafter SCL) for each turtle. The SCL covariates helped account for larger older turtles being more likely to emigrate from St. Joseph Bay and variation in p associated with body size for turtles that remained in the population. We natural-log-transformed SCL due to a right-skewed distribution and standardized to a mean of zero and SD of 1. We also included an indicator (dummy) variable for ϕ to account for mean differences between turtles marked at occasion 1 and turtles marked at occasion 2 or 3 (hereafter cohort g 1 and 2, where 1 is the reference level). The hierarchical model can be written in linear form as follows:

$$\text{logit}(\phi_{i,t}) = \alpha_t + \alpha_{1g[i]} + \beta_1 \text{SCL}_i,$$

$$\alpha_t \sim N(\mu_\alpha, \sigma_\alpha^2),$$

$$\text{logit}(p_{i,t}) = \omega_t + \beta_2 \text{SCL}_i,$$

$$\omega_t \sim N(\mu_\omega, \sigma_\omega^2),$$

where α is estimated apparent survival for a juvenile green turtle of mean SCL in cohort 1, ω is estimated recapture probability for a juvenile green turtle of mean SCL in cohort 1, α_1 is the mean difference in ϕ for cohort 2, β_1 and β_2 are slopes that represent estimated changes in ϕ and p with a 1 SD increase in SCL on the natural-log scale, μ is the occasion group mean, and σ^2 is the variance.

We report estimates as posterior distributions with 90% highest density intervals (HDIs). The mode for each coefficient is the most likely estimate, but all values in the posterior distribution have some degree of credibility. The HDIs contained credible values with a total probability of 90%. Unlike traditional confidence intervals, both

posterior distributions and associated HDIs represent probabilities that provide relative support for plausible parameter values (Kruschke & Liddell, 2019). The cohort indicator variable and SCL slopes were retained in the model if the HDI did not overlap zero. The mean estimated ϕ and p across occasions for cohort 1 are reported as the mean of the modes \pm SD on the 0–1 scale.

We fit the model using the program JAGS (Plummer, 2003) called from the package jagsUI (Kellner, 2018) within the statistical software R (version 4.1.0; R Core Team, 2021). We used a direct, hierarchical (i.e., state-space) construction of the CJS model likelihood (Gimenez et al., 2007; Kéry & Royle, 2020). Vague gamma priors were used for occasion SDs, with truncated vague normal priors for other parameters (Kéry & Schaub, 2012). Posterior distributions were estimated with Markov chain Monte Carlo methods using four chains of 50,000 iterations each ran in parallel after a 25,000-iteration burn-in phase (thinning = 100). We calculated HDIs using the R package HDInterval (Meredith & Kruschke, 2018). We assessed model convergence using a potential scale reduction factor (\hat{R} ; Brooks & Gelman, 1998) and trace plots. We considered adequate convergence an $\hat{R} < 1.05$ and a “grassy” trace plot for all parameters (Kéry & Schaub, 2012). Binary responses are not aggregated in the state-space formulation of the CJS model; thus, a posterior predictive check was not possible (Conn et al., 2018; Kéry & Schaub, 2012; McCullagh & Nelder, 1989). A formulation that uses aggregated responses (e.g., m -array) does not accommodate individual-level covariates (Brooks et al., 2000; Kéry & Royle, 2020; Kéry & Schaub, 2012).

RESULTS

Cold-stun mark and recapture data

A total of 1487 juvenile green turtles were marked across occasions 1–3 (80% in occasion 1), with generally higher return rates for turtles marked at occasions 2 and 3 (Table 1). As expected, catch rates were higher at occasions 1 and 4. Mean SCL was ~ 4 and ~ 2 cm greater at occasion 1 than at occasions 2 and 3, respectively, with a similar spread of measurements for all marking occasions. Return rates of occasion 1 turtles were higher at occasion 2 (0.10) than at occasions 3 and 4 (0.02 and 0.01, respectively). Occasion 4 return rates were higher for occasion 2 and occasion 3 (0.04 and 0.15, respectively) turtles than for occasion 1 turtles. The return rate of occasion 2 turtles at occasion 3 was only 0.01. However, the number of recaptures increased from occasions 3 to 4 for occasion 2 turtles but decreased for occasion 1 turtles (i.e., a greater proportion of occasion 2 turtles were

present during occasion 3 but not captured). Seven turtles from occasion 1 were recaptured twice. No cohort 1 turtles were encountered in all three recapture occasions. No turtles from cohort 2 were recaptured twice. In addition to the 12 USGS resightings included in the survival model, six additional cold-stunned turtles from cohort 1 were encountered between fall 2011 and winter 2012.

Survival modeling

The mean estimated ϕ for cohort 1 among open intervals between occasions was 0.32 ± 0.08 (Table 2, Figure 2). The posterior distribution for the interval between occasions 1 and 2 had most support for $\phi \sim 0.4$, with values ~ 0.3 – 0.6 contained in the 90% HDI (Figure 2). There were little support in the posterior distribution for $\phi > 0.8$ and no support for values of $\phi < 0.2$. Apparent survival probability was lowest for cohort 1 from occasions 2 to 3. The posterior distribution for the interval between occasions 2 and 3 had strong support for $\phi \sim 0.2$, with lower uncertainty (i.e., higher precision) than for intervals between other occasions. Values of $\phi \sim 0.1$ – 0.4 were contained in the 90% HDI. There was little support for $\phi > 0.5$. The posterior distribution for the interval between occasion 3 and occasion 4 had the most support for $\phi \sim 0.3$ but with higher uncertainty than for intervals between other occasions. Values of $\phi \sim 0.2$ – 0.6 were contained in the 90% HDI. There was some support for $\phi < 0.2$ but little support for $\phi > 0.7$.

TABLE 2 Cormack–Jolly–Seber model estimates of apparent survival probability ϕ and recapture probability p . Estimates are reported on the logit scale as the mode with a 90% highest density interval (HDI). Time-varying occasion estimates and straight carapace length (SCL) relationships are reported on the 0–1 scale in Figures 2 and 4, respectively.

Coefficient	Mode (90% HDI)
$\phi (t \pm 1)$	
Occasion 1	−0.44 (−1.05, 0.23)
Occasion 2	−1.16 (−1.95, −0.45)
Occasion 3	−0.67 (−1.61, 0.33)
Cohort 2	0.53 (0.16, 1.29)
SCL	−0.58 (−0.95, −0.23)
$p (t)$	
Occasion 2	−0.97 (−1.52, −0.38)
Occasion 3	−1.75 (−2.57, −1.00)
Occasion 4	−0.98 (−1.83, −0.01)
SCL	0.95 (0.45, 1.46)

The mean apparent survival probability was higher for cohort 2 than for cohort 1. The 90% HDI for this cohort indicator variable did not overlap zero and supported a positive relationship (Table 1). The probability of remaining in the population was higher for cohort 2 both from occasions 2 to 3 and from occasions 3 to 4 (Figure 2).

Relatively few turtles from cohort 1 likely remained in the population by occasion 3. Conservative estimates of ϕ (i.e., higher end of uncertainty) suggested $\sim 25\%$ of turtles from cohort 1 remained in the population by occasion 3 and $\sim 15\%$ by occasion 4 (Figure 2). Less conservative estimates of ϕ suggested $< 5\%$ of cohort 1 turtles remained in the population by occasion 3.

The mean estimated p for cohort 1 among occasions was 0.23 ± 0.07 (Table 2, Figure 2). Recapture probability was similar for occasions 2 and 4, with most support for $p \sim 0.30$. The 90% HDI for occasion 2 contained values of $p \sim 0.2$ – 0.4 , with no support for $p > 0.5$. Uncertainty in p was higher for occasion 4 (90% HDI ~ 0.2 – 0.5), with some support for $p > 0.5$. Recapture probability was lower for occasion 3, with similar precision as occasion 2. The 90% HDI for occasion 3 contained values of $p \sim 0.1$ – 0.3 , with no support for $p > 0.5$.

There was a linear relationship between both ϕ and p with SCL but with slopes in opposite directions. The 90% HDI for the ϕ SCL slope did not overlap zero and supported a negative relationship (Table 1). On average, relatively large turtles (i.e., SCL > 60 cm) had ~ 0.4 lower ϕ than relatively smaller turtles (i.e., SCL < 30 cm; Figure 3). Uncertainty was similar in the relationship with apparent survival across turtles of all body sizes. The 90% HDI for the p SCL slope also did not overlap zero but supported a positive relationship (Table 1). On average, relatively large turtles that remained in the population had ~ 0.5 higher p than relatively smaller turtles (Figure 3). However, there was higher uncertainty in the SCL relationship for larger turtles. Collectively, the SCL relationships suggest smaller turtles were more likely to remain in the population across occasions but were less likely to be recaptured.

DISCUSSION

Our findings indicated a small percentage of juvenile green turtles rescued during a severe cold stun in January 2010 remained in the St. Joseph Bay population 4 years later. About half the turtles likely remained 1 year later, but 10%–20% likely remained by 2014 and $< 5\%$ by 2018. Apparent survival was low relative to the prevailing thought about juvenile green turtle residency time in temperate foraging areas (see more detailed discussion below).

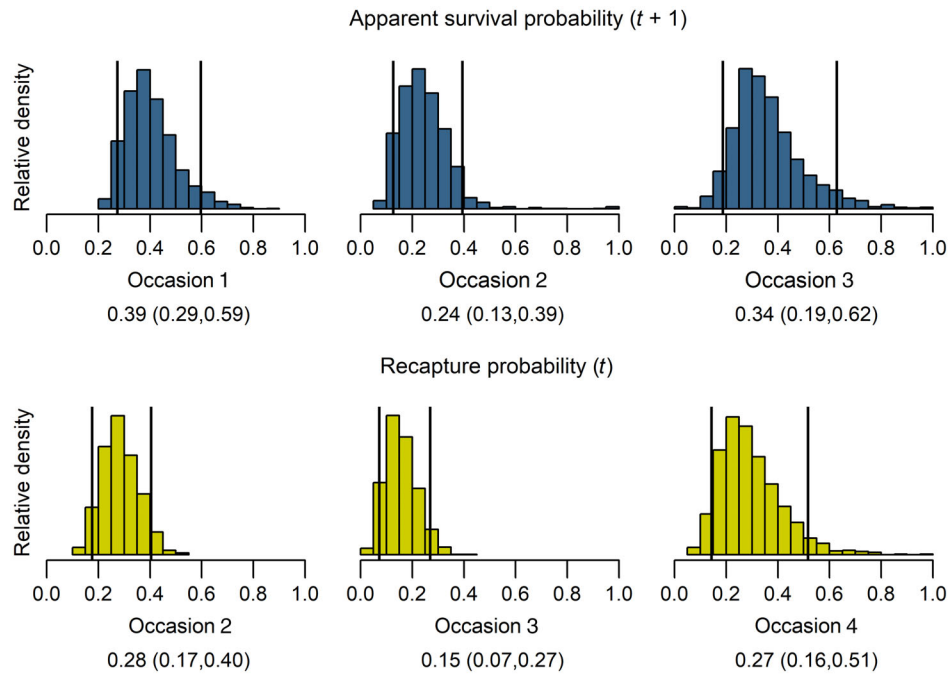


FIGURE 2 Posterior distributions for cohort 1 apparent survival probability ϕ (blue histograms in upper panels) and recapture probability p (yellow histograms in lower panels) approximated on the 0–1 scale. Values below the x-axis labels are the mode with a 90% highest density interval (HDI). Vertical lines approximate HDI cutoffs. Estimates of ϕ and p for each occasion (t) represent a juvenile green turtle from cohort 1 with mean notch-to-notch straight carapace length at marking on the natural-log scale (38.30 cm).

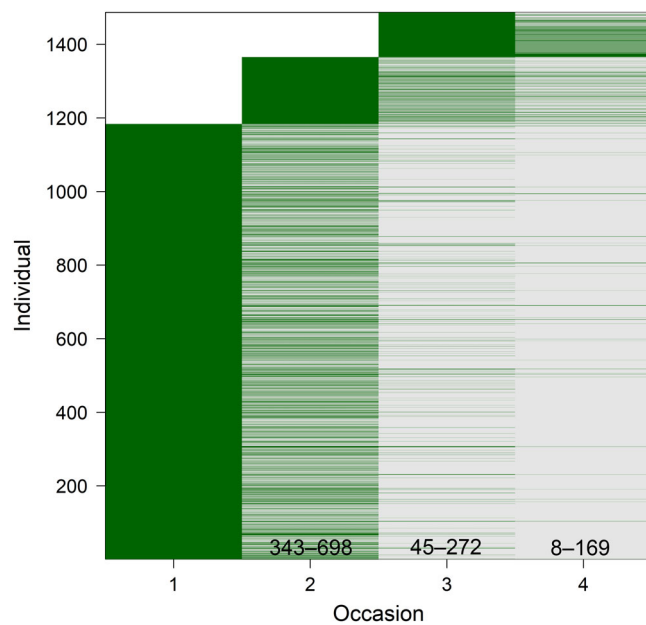


FIGURE 3 Latent-state z transition matrix for marked juvenile green turtles. Green is “alive” (marking occasion), and gray is “dead,” with lighter shades of green representing lower apparent survival probability ϕ in the open interval between occasions. Numbers above the x-axis approximate the number of turtles remaining from cohort 1 at occasions 2, 3, and 4 using endpoints from 90% highest density intervals for ϕ (Figure 1).

Although limited by small sample size, the results also suggest higher apparent survival for rescued turtles in the two subsequent milder cold stuns. The observed data also support lower apparent survival for turtles marked in occasion 1 (e.g., lower return rate in occasion 4).

An inherent challenge of any apparent survival study is differentiating between mortality and emigration (Kéry & Schaub, 2012; Lebreton et al., 1992). All animal populations have some degree of emigration; thus, true survival is always higher than apparent survival. The difference may not be critical from a management perspective (e.g., apparent survival represents a component of population turnover regardless of the mechanism). However, the ecological explanation is largely speculative when, most commonly, the fate is only known for individuals recaptured during the last occasion. The USGS resightings between cold stuns in St. Joseph Bay did not discover any mortalities from the January 2010 cold stun (M. M. Lamont, personal observations), and recovery efforts following the cold stuns found only five marked dead turtles (all marked in occasion 4; A. Foley, unpublished data). Thus, emigration more likely explains low apparent survival for occasion 1 turtles than delayed mortality. Emigration was also shown to better explain juvenile green turtle apparent survival than mortality in a 10-year study in the temperate Indian River Lagoon, FL, USA (Sterner, 2007).

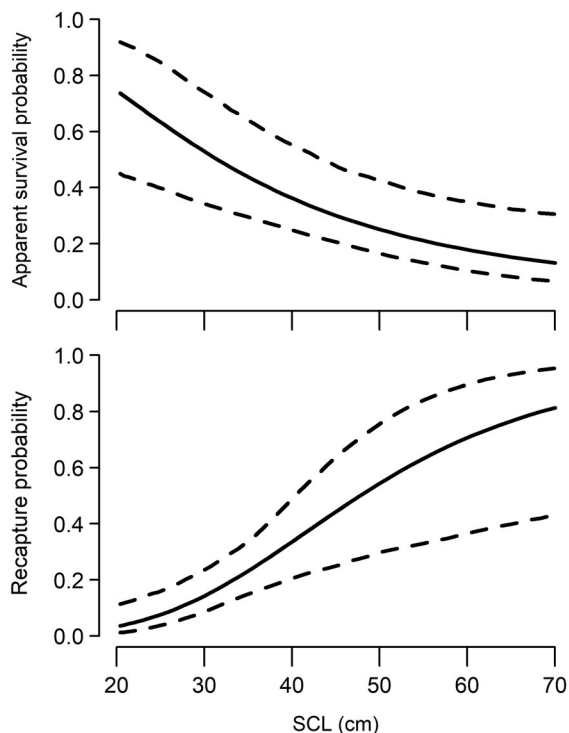


FIGURE 4 Relationships with notch-to-notch straight carapace length at marking (SCL) for juvenile green turtle apparent survival probability ϕ and recapture probability p . The slopes (solid lines) represent the mean change in ϕ and p on the 0–1 scale across all turtles with increases in SCL. Dashed lines are 90% confidence limits. The curvature in the lines is an artifact of both the approximation of the probability from the modeled logit scale and the back-transformation of SCL from the natural-log scale.

Potential reasons for the emigration of cold-stunned juvenile green turtles in St. Joseph Bay include a reduction in food availability, typical annual turnover associated with life history characteristics, and some behavioral response to the extreme weather event. Shorter term studies (i.e., <3 year) indicate that juvenile green turtles exhibit site fidelity to foraging areas in St. Joseph Bay (Lamont et al., 2015, 2018; Lamont & Johnson, 2021), temperate areas of the Florida Atlantic coast (Kubis et al., 2009; Mendonca, 1983), and other regions globally (e.g., Hancock et al., 2018; Hart & Fujisaki, 2010; Seminoff, Resendiz, & Nichols, 2002; Shimada et al., 2014; Siegwalt et al., 2020). However, variation in the temporal extent of residency within and among regions is not well known, with information on green turtle movement dynamics particularly limited in temperate areas. Migrations from foraging areas have been documented for a small number of juvenile green turtles (Godley et al., 2003; Sanchez et al., 2020), including in response to food availability (Carman et al., 2012). Juvenile green turtles in St. Joseph Bay primarily forage on turtle grass (Foley et al., 2007), but diets include invertebrates (Williams et al., 2014). Studies

have only observed mild effects of cold snaps on seagrasses (Adams et al., 2017; Lirman et al., 2014), but high mortalities have been reported for marine invertebrates (Colella et al., 2012; Crickenberger & Moran, 2013; Roberts et al., 1982). Decreased invertebrate abundance has also been associated with decreased water temperature in near-shore areas of St. Joseph Bay (Beddingfield & McClintock, 1994). However, we are not aware of any studies documenting changes in St. Joseph Bay invertebrate populations following the January 2010 cold stun. Although juvenile green turtles are presumed long-term residents in St. Joseph Bay, actual annual population turnover is not known. Higher emigration that is currently presumed could result in similar apparent survival as the occasion 1 turtles. It is also plausible that this subpopulation of turtles had some unknown behavioral response to the severe cold stun or rescue procedures (or both) that caused unusually high emigration. In particular, some turtles were known to experience cold stuns in two consecutive winters (i.e., occasion 2 recaptures). The rehabilitation process itself (i.e., transport and excessive handling) can lead to residual stress and altered behavior (McNally et al., 2021), which also may have led to some degree of unknown delayed mortality or high emigration. Speculation on mechanisms is difficult without knowing the fate of more cold-stunned individuals or characteristics of the broader St. Joseph Bay green turtle population.

Our results are not directly comparable to sea turtle apparent survival estimates reported by other researchers. These studies typically focus on annual survival, most commonly reported as constant rather than time-dependent (e.g., Bjorndal et al., 2003; Braun-McNeill et al., 2007; Chaloupka & Limpus, 2002). Modeling apparent survival for a single age class and accounting for individual variation due to size (i.e., a surrogate for age) reduced the chance of bias with unequal time intervals between occasions (Sanz-Aguilar et al., 2019). However, the unequal intervals between cold stuns (the nature of the event) prohibited annual estimates and assuming time-constant apparent survival was not consistent with the data or study objectives. A constant annual survival estimate also may not, in itself, be a useful metric for long-lived species such as sea turtles (Chaloupka & Limpus, 2002). Our single annual apparent survival estimate (i.e., the interval between occasions 1 and 2) is similar to time-constant estimates for juvenile green turtle populations in the Bahamas (~0.7; Bjorndal et al., 2003) but lower than for a Great Barrier Reef population (~0.9; Chaloupka & Limpus, 2005). Annual survival for juvenile green turtles is not known in St. Joseph Bay or the broader northern Gulf of Mexico. However, we emphasize our cumulative results better represent estimates of the number of turtles remaining across cold stuns than year-to-year apparent survival.

Conservation implications

Understanding responses of animal populations to environmental change is fundamental to ecology and essential to sound conservation and management strategies. Climate change presents a unique threat to sea turtle populations. Sea turtles may be increasingly vulnerable to cold stuns due to the combination of a northward range expansion in response to long-term warming and the expected increase in cold snaps at middle latitudes. Extreme weather events represent an opportunity to study both short- and long-term effects on abundance, survival, and population demographics (Gill, 2015; Jentsch et al., 2007). However, the uncertainty around the timing and location of cold stuns makes planning and study design challenging. Our study reports important baseline information about apparent survival of cold-stunned juvenile green turtles over a prolonged time period. The findings help provide a foundation for future studies that examine changes in juvenile sea turtle populations following cold stuns in the northern Gulf of Mexico. Although mechanisms are speculative, our findings do suggest lower apparent survival for cold-stunned juvenile green turtles than would be expected based on prevailing expert opinion. The basic survival information also provides a comparison for juvenile sea turtle cold-stun studies in other temperate regions. In addition, the general modeling approach, in conjunction with modified survey designs, can be expanded to additional ecological questions. Cold stuns provide a unique opportunity to increase capture efficiency relative to conventional sea turtle sampling. Sound long-term monitoring strategies that maximize these data promote more comprehensive information about delayed sea turtle responses to cold stuns. Further, sea turtle population characteristics, in general, are not well known (Ceriani et al., 2019; Osland et al., 2021; Putman et al., 2020). Cold-stun recapture data, in conjunction with effective sampling between events, can also provide important population information.

An optimized juvenile green turtle mark–recapture monitoring strategy relies on strategic sampling between cold stuns. An emphasis on increasing the number of marked turtles in the total population has numerous advantages. A turtle first marked during a cold-stun rescue provides minimal information about the broader population because the nature of the event (e.g., thermal shock and excessive handling) likely severely violates the fundamental assumption of no differences between marked and unmarked individuals. We show that recapture probability was likely adequate during cold stuns for abundance estimation (i.e., >20% of remaining turtles). However, useful abundance estimates also rely on a large number of marked individuals (ideally >25% of the

remaining population; Lockwood & Schneider, 2000). A larger number of marked individuals in the total population can also provide a control group to compare survival and abundance with cold-stunned turtles. More precise survival estimates could be achieved through a joint-data mark–recapture design that fully incorporates juvenile green turtle resightings with different sampling methods between cold stuns. For example, a general Barker survival model (Barbour et al., 2013; Barker, 1997) combines a CJS model with spatially replicated resightings during open periods and allows for temporary emigration. This approach does introduce up to five additional model parameters (i.e., more complexity), and unbiased survival estimates rely on high return rates during resightings (Barker, 1997). Future cold-stun survival studies could also identify differences in emigration rates between cold-stunned turtles and the general population through tracking (e.g., Bjørndal et al., 2003; Braun-McNeill et al., 2007). The practical implementation of a monitoring strategy for juvenile green turtles is, of course, site- and study-specific, and inherently constrained by time, available labor, and other logistics. However, more refined sampling designs and associated population estimation methods have increased flexibility (e.g., relaxed assumptions and increased ability to deal with model violations).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are sensitive and cannot be provided publicly. Requests to access the datasets should be directed to mlamont@usgs.gov at the US Geological Survey Wetland and Aquatic Research Center (<https://www.usgs.gov/centers/wetland-and-aquatic-research-center>) and allen.foley@myfwc.com at the Florida Fish and Wildlife Conservation Commission (<https://myfwc.com/about/inside-fwc/nc/>). The model code (Mollenhauer, 2022) is available from Zenodo: <https://doi.org/10.5281/zenodo.6807867>.

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