



Growth rates for immature Kemp's ridley sea turtles from a foraging area in the northern Gulf of Mexico

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ABSTRACT: Examining vital rates helps clarify how environmental characteristics, biological resources and human activities affect population growth. Carapace lengths were gathered for 241 Kemp's ridley *Lepidochelys kempii* sea turtles that were marked and recaptured ($n = 23$) between 2011 and 2019 at a foraging location in northwest Florida, USA. There was a strong correlation between length, width and weight of captured turtles. Mean \pm SD size of all captured turtles was 36.6 ± 7.6 cm. Mean recapture interval was 499 ± 475.4 d. Straight-line carapace lengths at initial capture ranged from 20.6 to 53.3 cm. Growth rates from 0.21 to 12.44 cm yr^{-1} (mean 3.15 ± 2.64 cm) were documented and were greatest for turtles in the 20.0–29.9 cm size class. Growth rates from northwest Florida were slower than those reported from other sites in the Gulf of Mexico. These results indicate that Kemp's ridleys recruit from oceanic habitat into coastal bays in northwest Florida, where they remain until they reach adulthood. However, some adult-sized turtles may continue to use the nearshore habitat. A gradient in growth rates in the Gulf of Mexico may occur from faster growth in the south to slower growth in the north. Fine-scale variations in resources and environmental conditions may drive regional differences in growth rates, and research on what drives these differences is needed.

KEY WORDS: *Lepidochelys kempii* · Mark–recapture · Demographic · Endangered species · von Bertalanffy · Age estimates · Northwest Florida

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1. INTRODUCTION

Demographic parameters including growth rate, birth rate and recruitment are key factors influencing population growth. Examining these vital rates helps clarify how fluctuations in environmental characteristics, biological resources and human activities affect population growth (Ogut et al. 2011). They can also help evaluate impacts of environmental disasters, and the potential for those perturbations to drive long-term population declines (Bjørndal et al. 2011). In addition, long-term monitoring of population demographic rates highlights susceptible life-

stages, which allows targeted conservation efforts. This is particularly important for highly mobile species that utilize disparate habitats at different life-stages, such as sea turtles (McClellan & Read 2007).

Growth rates for sea turtles are difficult to obtain due to their variable somatic growth patterns, lack of phenological age-related traits and highly migratory nature (Bjørndal et al. 2011). Growth rates have typically been estimated through skeletochronology, which requires use of carcasses, and mark–recapture of live individuals (Bjørndal et al. 2013, Avens et al. 2017). Many factors may affect sea turtle growth, including sea surface temperature (Bjørndal et al.

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2017), body size (Bjorndal et al. 2013, Rees et al. 2013), foraging location (Piovano et al. 2011) and latitude (Bell & Pike 2012, Bjorndal et al. 2017). However, these factors may vary by location. For example, most studies have shown that growth varies by body size (Balazs & Chaloupka 2004, Kubis et al. 2009, Bjorndal & Bolten 2010, Bjorndal et al. 2013), although Braun-McNeill et al. (2008) found no relationship between body size and growth in loggerheads *Caretta caretta* from Core Sound, North Carolina (USA). In addition, Bjorndal et al. (2013) found variable growth rates for loggerheads from different foraging grounds, suggesting that resource quality and environmental factors, among other things, may regulate growth. Because of this, growth rates for sea turtles are not transferrable from region to region. Currently, population models used in the development of recovery plans for imperiled sea turtle species rely on accurate estimates of vital rates including growth (Heppell et al. 2003, National Research Council 2010, Galloway et al. 2016). These models are critical for effective management and could be improved with availability of data specific to geographic regions.

Kemp's ridley sea turtle *Lepidochelys kempii* is one of the world's most endangered sea turtle species. Kemp's ridleys historically nested in only 1 location along the western Gulf of Mexico (GoM) coast. By the 1980s, only a few hundred nesting females remained, due primarily to nest poaching and fishery bycatch (NMFS & USFWS 2015). A bi-national effort between the USA and Mexico resulted in an increase in the number of nesting females; however, this steady growth in nest numbers suddenly ceased in 2010, coincident with the *Deepwater Horizon* oil spill (NMFS & USFWS 2015). Although Kemp's ridleys were potentially impacted by the oil spill, females nesting in Mexico in 2010 would have already arrived at the nesting beach before the spill occurred, and as such, direct impacts to those individuals may have been minimal. Therefore, other factors have been suggested as drivers of this decline, including density-dependent factors resulting from rapid population growth (NMFS & USFWS 2015).

Although Kemp's ridleys nest almost exclusively on beaches in the western GoM, immature turtles forage throughout the GoM and the northwestern Atlantic. In general, growth rates in the GoM (Schmid & Witzell 1997) are greater than in the Atlantic (Morreale & Standora 1998, Schmid & Woodhead 2000). However, variation has been observed among foraging sites, even within the same ocean basin. The growth rate of turtles from Gullivan Bay in South

Florida (Witzell & Schmid 2004) was higher than that of individuals farther north in Cedar Key, Florida (Schmid & Witzell 1997). Documenting these site-specific variations in growth rate is critical for management, yet growth data for immature Kemp's ridleys at other foraging areas in the GoM are lacking. Here we present growth data from a long-term mark-recapture project at an important foraging site for immature Kemp's ridleys in northwest Florida.

2. MATERIALS AND METHODS

St. Joseph Bay (SJB), located in northwest Florida in the northern GoM (Fig. 1), covers approximately 26 000 ha and is surrounded by mostly undeveloped land and the small town of Port St. Joe (population 3500; FLDEP 2008). It has a mean depth of 7 m, with the greatest depth (13.3 m) at the northern end and the shallowest (1 m) at the southern end (FLDEP 2008). Sea grass beds cover approximately one-sixth of the Bay (4000 ha) and are most abundant in the shallow southern end (FLDEP 2008). The most abundant seagrass species is *Thalassia testudinum*. This relatively pristine seagrass habitat provides resources for foraging sea turtles including loggerheads, green turtles *Chelonia mydas* and Kemp's ridleys (Lamont & Iverson 2018) and makes SJB an important developmental area for immature Kemp's ridleys. Mass stranding events due to extreme cold resulted in the stranding of >1700 turtles (n = 63 Kemp's ridleys) in 2010 and >1200 turtles (n = 48 Kemp's ridleys) in 2018; these events highlight the large number of immature turtles that utilize SJB (Avens et al. 2012).

Marine turtles were captured year-round between 2011 and 2019 using a set net or dip net, or by hand. All captured turtles were individually marked with a metal Inconel tag placed along the trailing edge of each front flipper and a passive integrated transponder (PIT) tag placed subcutaneously in the left shoulder. Turtles were measured in straight carapace length (SCL; measured from the nuchal notch to the left posterior tip of the carapace) and width (SCW) using calipers. Weight was determined by placing the turtle in a harness and hanging the harness from a hand-held Pesola spring scale.

Annual growth rates for recaptured Kemp's ridleys were calculated using the following formula:

$$G = [(\Delta\text{length})(\text{days}^{-1})] \times 365 \quad (1)$$

where G is growth rate (cm yr^{-1}), Δlength is the difference in SCL (cm) between capture and recapture,

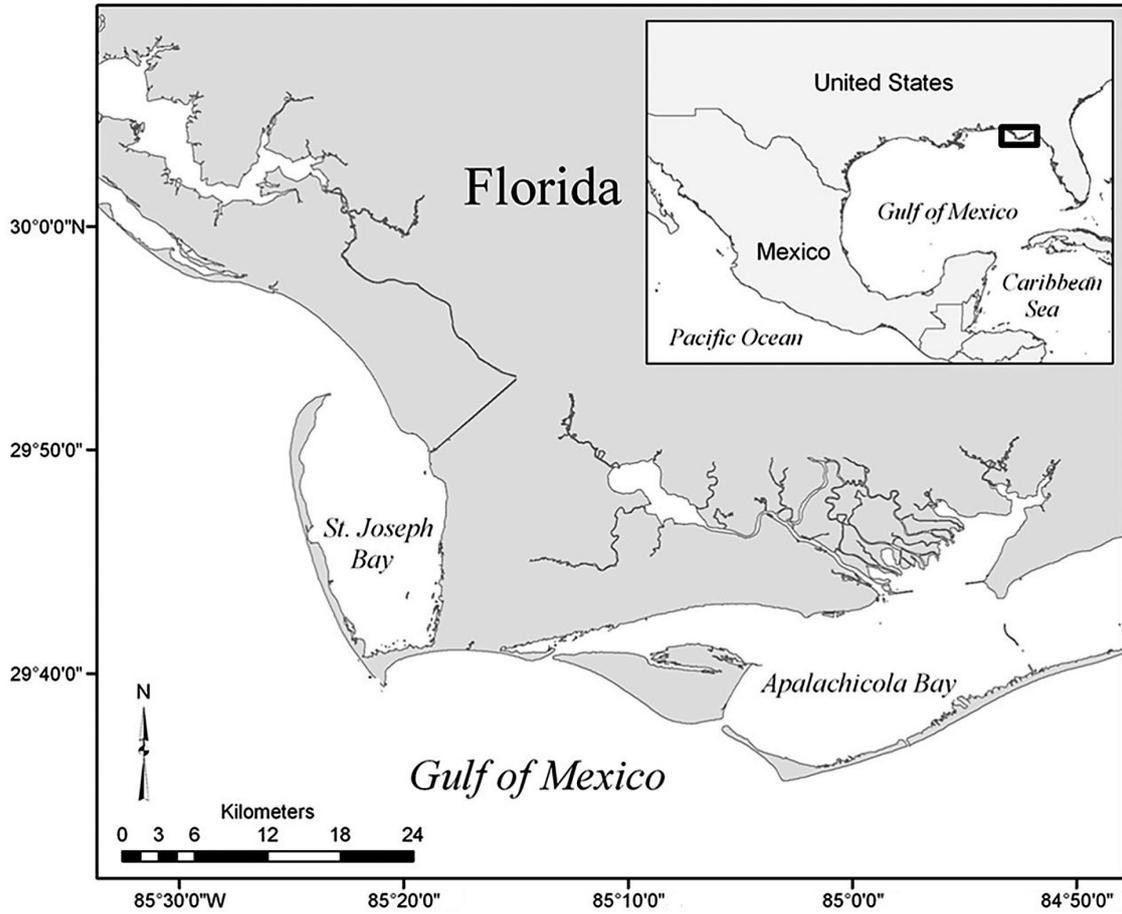


Fig. 1. St. Joseph Bay, Florida, USA, where immature Kemp's ridley turtles were captured and measured between 2011 and 2019 to estimate growth rates

and days is the number of days between capture and recapture.

We ran the von Bertalanffy growth model with unknown ages to estimate the growth rate of recaptured immature Kemp's ridleys from SJB. The von Bertalanffy growth equations are expressed as:

$$L_t = a(1 - be^{-kt}) \quad (2)$$

where L is the length at age t , a is asymptotic length (defined as the upper bound estimate of immature growth), b is a parameter related to size at hatching, and k is the intrinsic growth rate. The von Bertalanffy growth interval equation was modified by Fabens (1965) to estimate growth parameters of animals of unknown age based on recapture data. The Fabens growth equation is:

$$L_r = a - (a - L_c)e^{-kd} \quad (3)$$

where L_r is the length at recapture, a is asymptotic length, L_c is the length at first capture, k is the intrinsic

growth rate, and d is the time interval between captures.

The von Bertalanffy equation was fitted to the Kemp's ridley growth data with a non-linear least-squares regression procedure. The Fabens equation does not contain an estimate of b , which is necessary to complete the von Bertalanffy model. This parameter was estimated using Eq. (2) simplified to:

$$b = 1 - L_0/a \quad (4)$$

where L_0 is the mean hatchling carapace length of 4.4 cm (Márquez 1994).

We used the Gauss-Newton method (PROC NLIN, SAS 9.4) to estimate the von Bertalanffy nonlinear equation. Because short recapture intervals can be biased, we followed Schmid & Witzell (1997) and constructed growth models using 4 different recapture intervals: >90 d apart, >180 d apart, >270 d apart and >360 d apart. If a turtle was recaptured more than once, the last recapture value was used.

We used the root mean square error (RMSE) to identify the model with the best fit (e.g. recaptures >90 vs. >180 d apart). Also, the asymptotic length was used as a guide for model fit based upon published estimates for minimum and mean carapace length at sexual maturity (Shaver et al. 2016, Avens et al. 2017). An alpha value of 0.05 was used for all analyses.

3. RESULTS

From 31 May 2011 to 1 October 2019, we captured 493 turtles in SJB, primarily (76%) by hand. Of that total, we captured 241 (48.7%) Kemp's ridleys. Kemp's ridleys were captured in every month, with most captures occurring in July (22%) and October (21%). Mean \pm SD SCL of all 241 Kemp's ridleys was 36.6 ± 7.7 cm (range 20.6–53.3 cm; Fig. 2). We recaptured 23 individuals (9.5% recapture rate). Recaptures occurred in every month except January, June and November. Most recaptures occurred in July

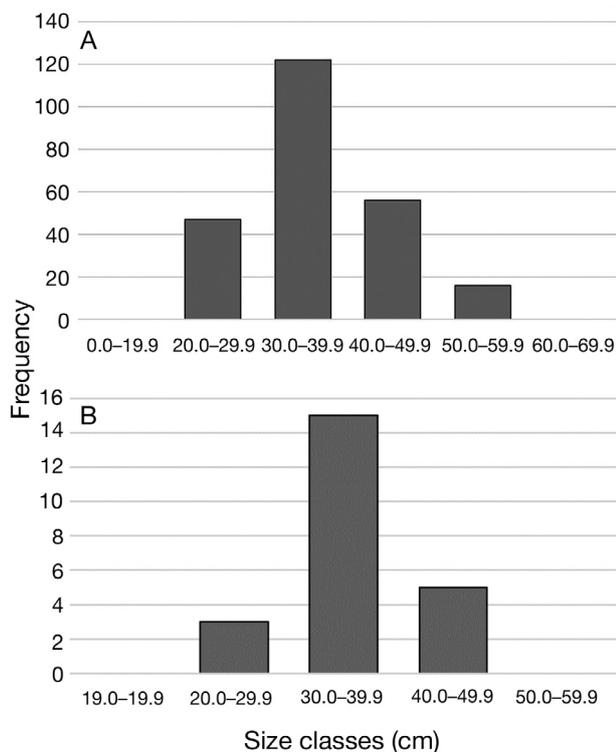


Fig. 2. Size classes of (A) all ($n = 241$) and (B) recaptured ($n = 23$) Kemp's ridley turtles from St. Joseph Bay in northwest Florida. Recaptured turtles were assigned to a size class based on the mean value of their size at capture and recapture. Note different scales on the y-axes

(23%) and October (27%). All recaptures occurred in SJB; to our knowledge, no Kemp's ridleys captured in SJB have been subsequently re-captured outside of SJB. Mean size and recapture data were calculated using the first and last capture only (Table 1). Mean size of all recaptured Kemp's ridleys (at recapture) was 37.6 ± 7.2 cm (range 21.7–53.3 cm). Mean recapture interval for all Kemp's ridleys was 499 d (range 6–1705 d; median 293 d).

Our initial analyses included 20 recapture intervals >90 d with a mean interval of 570 ± 470.3 d (range 129–1705 d). The mean size of these 20 individuals was 32.7 ± 5.8 cm (range 21.2–41.6 cm) at initial capture and 38.0 ± 7.5 cm (range 21.7–53.3 cm) at recapture. The mean observed change in size for these 20 individuals from initial recapture to final recapture was 5.2 ± 5.5 cm (range 0.1–20.6 cm).

However, the growth model failed to converge with these 20 recaptured intervals. The model was only successful after turtle W472 was removed from the analysis. This individual had the longest recapture interval (1705 d) and was the largest turtle at recapture (53.3 cm).

We ran the models with the remaining 19 recapture intervals >90 d. These 19 recaptures had a mean interval of 510 ± 397.6 d (range 129–1488 d). The mean size of these individuals was 32.7 ± 6.0 cm (range 21.2–41.6 cm) at initial capture and 37.1 ± 6.8 cm SCL (range 21.7–47.9 cm) at recapture. The mean observed change in size from initial capture to final recapture was 4.4 ± 4.3 cm (range 0.1–14.1 cm).

The mean annual growth rate for all 20 recaptures >90 d (including W472) was 3.15 ± 2.64 cm yr⁻¹ (range 0.21–12.44 cm). Growth rates varied among size classes (Table 2) and were lowest for the largest size class (40.0–49.9 cm SCL; 2.10 cm yr⁻¹; range 0.21–4.39 cm yr⁻¹) and greatest for the smallest size (20.0–29.9 cm SCL; 5.02 cm yr⁻¹; range 0.93–12.44 cm yr⁻¹). Mean age estimates of all recaptured turtles ($n = 23$) in SJB was 7.4 ± 2.3 yr (range 3.25–11.03 yr; Figs. 3 & 4).

The model for the 19 recaptures >90 d had a better fit (i.e. lower RMSE) and more realistic asymptotic length ($a = 75.49$ cm; see Section 4) than the model for >180 d and >360 d (92.01 and 98.7 cm, respectively; Table 3). The asymptotic length for >270 d ($a = 74.02$) was slightly more biologically realistic than the model for >90 d; however, the RMSE for >90 d was the lowest (2.002) and therefore considered the most appropriate model (Dunham 1978). Hence, the growth equation for Kemp's ridleys from SJB was:

$$L_t = 75.4862 \times [1 - 0.9417 \times \exp(-0.0858t)] \quad (5)$$

Table 1. Straight carapace length at first capture (SCL Cap) and last recapture (SCL Recap), recapture interval, growth rates and age estimated from non-linear regression of von Bertalanffy growth intervals for all recaptured Kemp's ridley sea turtles from St. Joseph Bay, Florida, USA

ID	PIT tag	SCL Cap (cm)	SCL Recap (cm)	Recap interval (d)	Growth (cm yr ⁻¹)	Estimated age (yr)
288	4C133A447C	36.3	36.4	53	0.7	7.0
316	4B693D7C7B	33.0	47.1	1488	3.5	10.7
324	4A0C236A09	31.4	31.9	298	0.6	5.7
362	900118001184476	47.6	47.9	334	0.3	11.0
363	985121021194990	26.8	31.4	135	12.4	5.6
364	985121026877167	26.8	27.4	129	1.7	4.6
371	900118001188800	31.1	33.5	397	2.2	6.1
373	985121026844102	27.8	33.1	478	4.0	6.0
382	900118001186401	21.2	21.7	196	0.9	3.3
389	900118001186644	33.2	35.2	290	2.5	6.6
395	985121026886613	30.4	30.4	6	0.0	5.3
398	900118001215133	34.6	37.3	289	3.4	7.2
401	985121026832095	30.2	33.8	293	4.5	6.2
405	985121026841404	34.6	37.5	291	3.6	7.3
408	900118001188446	34.7	45.1	1036	3.7	9.9
412	4C1336745A	44.5	44.6	172	0.2	9.7
413	900118001215639	37.9	38.7	258	1.1	7.7
440	900118001215414	30.4	43.0	892	5.2	9.1
472	900118001185252	32.7	53.3	1705	4.4	13.60
474	982000361993633	32.2	38.5	589	4.4	7.6
479	982000361969320	31.6	37.1	1008	3.9	7.2
553	982000364297745	32.4	41.0	1117	2.0	8.4
811	982000410285212	38.6	38.6	21	2.8	7.6

Table 2. Mean \pm SD growth rate by size class (straight carapace length) for all Kemp's ridley turtles recaptured >90 d apart ($n = 20$) in St. Joseph Bay, Florida, from 2011–2019. Individuals were assigned to a size class based on their mean size at capture and recapture

Size class (cm)	N	Mean growth (cm yr ⁻¹)
20–29	3	5.02 \pm 6.43
30–39	13	3.04 \pm 1.32
40–49	4	2.10 \pm 2.14

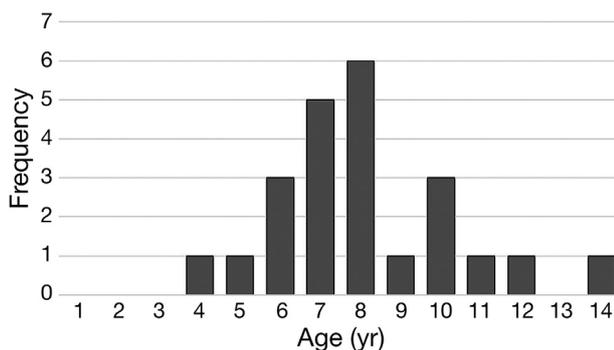


Fig. 3. Ages estimated from non-linear regression of von Bertalanffy growth intervals for Kemp's ridley turtles ($n = 23$) recaptured in St. Joseph Bay, Florida, between 2011 and 2019

4. DISCUSSION

Studies on growth of turtles have highlighted the importance of a dataset with a wide length distribution (Frazer et al. 1990, Schmid & Witzell 1997, Spencer 2002). However, in some species and at some locations, certain size classes are unavailable or have limited availability (Bjorndal et al. 2003). During post-nesting migration from beaches in southern Texas, telemetered female Kemp's ridleys utilized areas that were on average 20 km from shore in waters 26 m deep (Shaver et al. 2016). Although adults are occasionally present in bays or nearshore waters (Schmid & Tucker 2018), Kemp's ridleys captured in coastal bays from Texas (Seney & Landry 2011) to south Florida (Schmid & Tucker 2018) are dominated by immature individuals (Schmid & Witzell 1997, Schmid 1998). The largest Kemp's ridley captured in SJB during this study was 55.6 cm, and only 6.7% of all captures in SJB were >50 cm. The unavailability of larger individuals

in our study most likely results in biased estimates of asymptotic length (Frazer et al. 1990). In addition, our low recapture rate (9.6%) results in relatively few recaptures ($n = 23$) and recapture intervals >90 d ($n = 20$). Both Caillouet et al. (1995) and Schmid & Witzell (1997) acknowledged the limitations in their modeling efforts due to lack of larger turtles in their

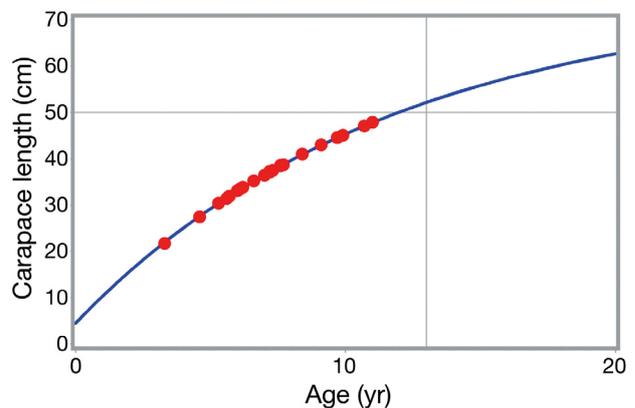


Fig. 4. Growth curves for immature Kemp's ridley turtles ($n = 23$) recaptured in St. Joseph Bay, Florida, between 2011 and 2019. Each red dot indicates the age (years) and straight carapace length (cm) for an individual turtle. Light grey lines highlight 50 cm carapace length for reference only

Table 3. Sample sizes and estimated values of asymptotic length (a) and its standard error (SE), intrinsic growth rate (k) and its SE and root mean square error (RMSE) for Kemp's ridley turtles in St. Joseph Bay, Florida

	N	a	SE	k	SE	RMSE
All recaptures >90 d	19	75.4862	40.4469	0.0858	0.0911	2.002
All recaptures >180 d	16	92.0066	84.2635	0.0598	0.0922	2.006
All recaptures >270 d	14	74.0209	42.6264	0.0903	0.1055	2.057
All recaptures >360 d	8	98.7227	170.6000	0.0552	0.1542	2.567

datasets, and we recognize the same limitations in our study. The lack of larger turtles also contributed to the model's inability to converge with the inclusion of the largest individual in our dataset (W472). Considering the value of demographic data to endangered species recovery (Dennis et al. 1991, Bjorndal et al. 2011), we believe that regardless of these limitations, this examination of 9 years of recapture data in SJB provides valuable information for Kemp's ridleys in the northern GoM.

The mean size of all captures in SJB was 35.5 cm SCL, compared to a mean size of 47.6 cm SCL captured by Schmid (1998) at Cedar Key, Florida. Recapture rates appear lower in SJB (9.5%) than for other regions and species (Schmid 1998, Witzell & Schmid 2004, McMichael et al. 2008, Kubis et al. 2009, Hart et al. 2016, Schmid & Tucker 2018), except for Barichivich (2006) who reported a 9.9% recapture rate. This may reflect variations in capture methods (hand capture versus tangle netting); however, Hart et al. (2016) documented a 65.2% recapture rate for green turtles in the Dry Tortugas using the same methods used to capture Kemp's ridleys in SJB (hand capture).

Growth rates for larger turtles (40.0–49.9 cm SCL) at Cedar Key were the fastest documented for that area (6.4 cm yr⁻¹). The greater proportion of these individuals captured in that area may have resulted in a faster overall growth rate as compared to SJB, where the majority of turtles captured were 30.0–39.9 cm SCL (2.52 cm yr⁻¹). Variations in size classes of turtles captured during growth studies could also affect overall growth rates at regional sites.

Patterns of growth by size class also differed in SJB. Most studies report slow growth from 20–30 cm and then a growth spurt from 30–40 cm (Morreale & Standora 1998, Schmid & Barichivich 2005, NMFS & USFWS 2015) although Witzell & Schmid (2004) reported the fastest growth (8.5 cm yr⁻¹) for the smallest turtles captured in south Florida. Similarly, we documented the fastest growth in the smallest turtles (20.0–29.9 cm; 5.02 cm yr⁻¹), although these

results reflect a large growth rate for 1 small individual (12.44 cm yr⁻¹) that grew from 26.8 to 31.4 cm in 135 d. This exceptional growth rate may represent sampling error; however, we also documented a corresponding increase in weight (1.9 kg) and straight carapace width (4.50 cm) for this individual. Witzell & Schmid (2004) suggested that faster growth in the smallest turtles may reflect

changes in diet as these small individuals move from oceanic to neritic foraging habitats.

Schmid (1998) reported the fastest growth rates for Kemp's ridleys in Cedar Key, Florida, in turtles 40.0–49.9 cm (6.2 cm yr⁻¹), whereas in SJB this size class represented the lowest growth rate (2.10 cm yr⁻¹). Again, some of this variation may be due to small sample sizes. We recaptured only 4 individuals in the largest size class. In addition, the mean size of turtles in the 40.0–49.9 cm size class in SJB was 43.6 cm. A second growth spurt, suggesting polyphasic growth in Kemp's ridleys, reportedly occurs around 46 cm, potentially associated with the onset of puberty (Snover 2008, NMFS & USFWS 2015) and/or a shift in developmental habitat (Chaloupka & Zug 1997, Schmid & Barichivich 2005). Perhaps the largest turtles in our study had not yet reached that stage and therefore we did not document the purported second growth spurt. More likely, however, is that these results highlight the variability in growth rates due to relatively small sample size and underrepresentation of larger size classes (Schmid 1998, Witzell & Schmid 2004, Schmid & Barichivich 2005, Barichivich 2006).

Sea turtle growth differs across regions due to a variety of factors that include environmental conditions, habitat quality, prey availability and turtle density (Bjorndal et al. 2003, 2017, Piovano et al. 2011). Even foraging sites in relative proximity to each other report variations in turtle growth (Diez & van Dam 2002, Kubis et al. 2009). Growth rates for Kemp's ridleys in SJB were slower than those reported elsewhere in the GoM and Atlantic (Schmid & Witzell 1997, Schmid 1998, Snover et al. 2007). St. Joseph Bay is located approximately 65 km north and 260 km west of Cedar Key, where Schmid (1998) reported a mean growth rate of 5.4 cm yr⁻¹ for immature Kemp's ridleys, compared to the mean 3.15 cm yr⁻¹ from this current study. Mean sea surface temperature (SST) in early summer (June) in Cedar Key was 1.4°C warmer than in Apalachicola Bay (approximately 35 km east of SJB), and mean SST in fall

(October) was 2.9°C warmer in Cedar Key than in Apalachicola Bay (Stations 8727520, 8728690). In addition, mean growth rates from southwest Florida were larger than those reported from both locations (i.e. Cedar Key and SJB), at 6.5 cm yr⁻¹ (Witzell & Schmid 2004). This may reflect a gradient in Kemp's ridley growth rates increasing from south to north due to warmer water temperatures (Fig. A1 in the Appendix). Coleman et al. (2016) also documented relatively slow growth (2.74 cm yr⁻¹) for Kemp's ridleys captured at fishing piers in Mississippi Sound, although this may reflect differences in foraging resources (i.e. piers versus hard-bottom habitats; Rudloe & Rudloe 2005). However, several studies have examined growth rates of green and loggerhead turtles and have found no latitudinal effect on growth (Balazs & Chaloupka 2004, Chaloupka et al. 2004, Bjørndal et al. 2013).

In addition to mean monthly temperatures that are slightly cooler than more southerly foraging areas, marine turtles in SJB occasionally experience extreme cold temperatures that result in mass stranding events (Foley et al. 2007). These stranding events, termed 'cold stunning,' occur when SST drops below 10°C. These cold temperatures significantly affect sea turtle physiology, and the turtles become lethargic and float at the water's surface (Anderson et al. 2011, Avens et al. 2012). Some of the largest cold-stunning events in the USA have occurred in SJB (Foley et al. 2007, Avens et al. 2012). Although these events appear to affect the physiology of turtles, at least in the short-term (e.g. <1 yr; Innis et al. 2009), exposure to extreme cold events in SJB does not appear to affect growth rates of green turtles (McMichael et al. 2008, Avens et al. 2012). The limited satellite tracking of immature Kemp's ridleys in SJB indicated that individuals may leave the bay in winter but, rather than migrate south along the coast, they remain in offshore waters in the northern GoM as proposed by Ogren (1989) (Rudloe et al. 1991, Lamont & Iverson 2018). Although impacts of cooler water temperatures and extreme cold events have not yet been evaluated for Kemp's ridleys, these factors may contribute to slower growth rates for Kemp's ridleys in SJB versus those at more southerly foraging sites (Witzell & Schmid 2004).

Differences in prey availability and quality are often considered a primary driver of growth rates (Diez & van Dam 2002, Kubis et al. 2009). Immature Kemp's ridleys have a broader diet than adults, with the latter foraging predominately on blue crabs *Callinectes sapidus* (Shaver 1991). In the GoM, immature Kemp's ridleys forage on multiple crab species but

also on mollusks, fish, benthic tunicates and vegetation (Shaver 1991, Witzell & Schmid 2005, Schmid & Tucker 2018). Unfortunately, no diet data exist for Kemp's ridleys in SJB. In Northwest Florida, Kemp's ridleys have been documented using seagrass, mudflat and sandflat habitats equally (Rudloe et al. 1991), whereas in Cedar Key, Kemp's ridleys used rock outcroppings at a higher proportion than seagrass or oyster reef habitat (Schmid et al. 2003). Differences in habitat use may reflect variations in diet, which may in turn result in different growth rates.

Our growth model for recaptures >90 d predicted an asymptotic length of 75.5 cm SCL for Kemp's ridleys in SJB. This estimate is larger than the mean carapace length of 63.3 cm for nesting females reported by Shaver et al. (2016) and slightly larger than the minimum size of 57.2 cm SCL and a maximum size of 75.2 cm SCL (Shaver et al. 2016). Frazer et al. (1990) suggested that biologically realistic estimates of asymptotic length should be slightly larger than the mean length of the adult population; however, our estimate appears to be very close to the upper size-limit for nesting females (Shaver et al. 2016). Estimating yearly growth rates from short-term recaptures amplifies measurement error (Schmid 1995). Extremely large or negative growth rates typically result from short recapture intervals. Our mean recapture interval, however, was 499 d, with 5 recaptures >1000 d. These long recapture rates also highlight the importance of SJB as a resident foraging area for immature Kemp's ridleys; fidelity by immature Kemp's ridleys has also been demonstrated for other important foraging habitats (Schmid 1998, Schmid et al. 2003, Seney & Landry 2011, NMFS & USFWS 2015).

Avens et al. (2017) used skeletochronology to estimate a mean size at sexual maturity of 61.3 cm for Kemp's ridleys in the GoM and mean age at sexual maturity of 12.2 yr. Our largest turtle recaptured was estimated to be 13.6 yr. The size of this individual (53.3 cm) falls below the minimum size for nesting females reported by Shaver et al. (2016; 57.2 cm) and is exactly the minimum size at sexual maturity reported by Avens et al. (2017), which indicates that this individual may not have been reproductively mature. The relatively slow growth we documented for immature Kemp's ridleys in SJB may have resulted in higher age estimates by the model (see Table 2). There is no clear break in carapace size between immatures and adults, which suggests a relatively long phase for puberty in Kemp's ridleys (Craven et al. 2019) and complicates the use of carapace size alone in assigning life-stages for captured turtles. In addition, the small sample size and lack of

larger size classes in our dataset may have resulted in biased age estimates (Schmid & Witzell 1997).

That being said, without the ability to examine reproductive organs, we only have size data to infer sexual maturity. The largest individual we captured in SJB was 55.6 cm, which suggests adult Kemp's ridleys are not using SJB. The dominance (74%) of individuals captured in the 30.0–49.9 cm size class supports the hypothesis that coastal bays such as SJB serve as an ontogenetic habitat for immature Kemp's ridleys (also see Rudloe et al. 1991). Once they reach sexual maturity around 60 cm SCL, they move out of this habitat and into adult foraging areas (NMFS & USFWS 2015). However, adult-size Kemp's ridleys have been documented at Cedar Key (Schmid 1998), Ten Thousand Islands (Schmid & Tucker 2018), Mississippi Sound (Coleman et al. 2017) and Laguna Madre, Texas (Metz & Landry 2016), and post-nesting Kemp's ridleys have been satellite tracked into coastal bays during migration (Shaver et al. 2016). These findings suggest that some overlap in habitat use may occur among adult and immature Kemp's ridleys in nearshore waters.

There also appears to be variation in the timing of ontogenetic movements by post-hatchlings. After hatchlings leave the nesting beach, Kemp's ridleys are believed to spend 2 yr in pelagic waters before moving into neritic habitat (NMFS & USFWS 2015). Our findings support Ogren (1989) and Collard & Ogren (1990), who also proposed recruitment of small Kemp's ridleys in northwest Florida coastal habitat. The mean size of Kemp's ridleys captured in oceanic habitat in the eastern GoM by Witherington et al. (2012) was 23.3 cm, and Putman & Mansfield (2015) captured Kemp's ridleys up to 29.9 cm in oceanic waters. The smallest turtle captured in SJB was 20.8 cm, and 47 (20%) captured individuals were smaller than 30 cm. These small individuals represent new recruits from oceanic to neritic habitat, and suggest that, although Witherington et al. (2012) and Putman & Mansfield (2015) documented individuals >25 cm still using oceanic habitat, some Kemp's ridleys recruit to immature foraging grounds in the northern GoM at a smaller size (<25 cm). This is also supported by Schmid (1995) and Schmid & Tucker (2018), who documented 21.5 and 24.2 cm SCL sized Kemp's ridleys off Florida's east coast and in the southeastern GoM, respectively.

The lower recapture rate for this species makes modeling growth parameters difficult. However, generating baselines and monitoring changes in these data are necessary as the climate changes, anthropogenic alterations to the environment occur (e.g.

dredging, installing jetties, etc.), and environmental disasters such as oil spills impact marine habitats (Bjorndal et al. 2011). Furthermore, studies examining fine-scale variations in resources that may drive regional differences in growth rates are needed.

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Appendix.



Fig. A1. Locations (red dots) where mean growth rates (black number, in cm yr^{-1}) for immature Kemp's ridley turtles have been reported in the northern and eastern Gulf of Mexico. From south to north: Gullivan Bay (6.3, Witzell & Schmid 2004); Cedar Key (5.4, Schmid 1998); Deadman's Key (4.2, Barichivich 2006); St. Joseph Bay (3.2, this study); and Mississippi Sound, MS (2.7, Coleman et al. 2016). Note that growth rates for Mississippi Sound were gathered from individuals caught hook-and-line on fishing piers

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