

A SEASONAL AND LATITUDINAL
ASSESSMENT OF EARLY GROWTH RATES
IN NORTHERN AND SOUTHEASTERN
LOGGERHEAD SEA TURTLES
(CARETTA CARETTA L.)

LESLEY STOKES

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GROWTH RATES IN NORTHERN AND SOUTHEASTERN
LOGGERHEAD SEA TURTLES (*CARETTA CARETTA* L.)

By

Lesley Stokes

A Thesis Submitted to the Faculty of

The Charles E. Schmidt College of Science

In Partial Fulfillment of the Requirements for the Degree of

Master of Science

Florida Atlantic University

Boca Raton, Florida

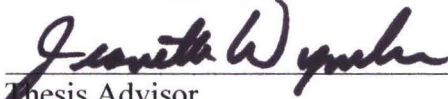
December 2003


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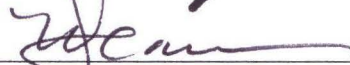
This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Jeanette Wyneken, Department of Biological Sciences, and has been approved by the members of her supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was received in partial fulfillment of the requirements for the degree of Master of Science.

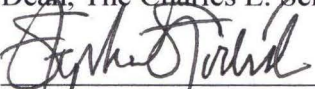
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ACKNOWLEDGEMENTS

I would like to thank my advisor Jeanette Wyneken for her effort, insight and patience, as well as committee members Peter Lutz and Michael Salmon for their thoughtful input and guidance. Allan J. Nash and Eileen Curtayne were extremely helpful with their statistical advice.

For their invaluable assistance with the project, I am extremely grateful to Jason Vaughan, Kimberly Blair and Neal Tempel (Florida Atlantic University). Special thanks to Jesse Marsh, Kelly Stewart, Craig Harms, Larry Crowder, Jerris Foote, Corie Baird, Charles Manire, Kirt Rusenko and the staff at the Gumbo Limbo Nature Center; Larry Wood, Chris Johnson, Kristie Grigg, Beverly Ball, Michael Bresette, Dean Bagley, Kelly Rogers, Stacy Kubitz, Rick Herren, Jim Weege, DVM, Jack Merlino (Boynton Fisherman Supply), and Jim Abernethy.

For their countless hours helping me feed turtles, I thank Carla Arantes, Sharon Azogue, Jeremy Conrad, Mertash Davari, Pricilla Goodwin, Melvin Lamar, Dean Monette, Jonathan Nava, Luis Ospina and Sean Smith.

I would like to acknowledge the following organizations for their assistance in providing hatchlings and data: Cape Lookout National Sea Shore, Cape Island Turtle Program, Duke University Marine Laboratory, Ecological Associates, Georgia DNR, Kiawah Island Turtle Program, Marinelife Center at Juno Beach, Mote Marine Laboratory, Quantum Associates (FPL), Sanibel-Captiva Sea Turtle Program, National Marine Fisheries Service, UCF Marine Turtle Program, Palm Beach County DERM, Miami-Dade County DNR, and NC Wildlife Commission.

Work was conducted under Florida Fish and Wildlife sea turtle permit number 073 to Jeanette Wyneken and under Florida Atlantic University IACUC # A0026. This research would not have been possible without the funding and support of the Environmental Protection Agency STAR grant GAD R82-9094 to J. Wyneken.

Without the encouragement and support of my family and friends, this would not have been possible. I would like to specially thank my husband, Gary, for his listening, love, cooking, and incredible patience and understanding.

ABSTRACT

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Title: A seasonal and latitudinal assessment of early growth rates in northern and southeastern loggerhead sea turtles (*Caretta caretta*)
Institution: Florida Atlantic University
Thesis Advisor: Dr. Jeanette Wyneken
Degree: Master of Science
Year: 2003

To improve our understanding of loggerhead life history, particularly factors affecting the duration of each age class and survivorship, detailed growth data must be interpreted. The purpose of this study was to investigate how temporal and spatial nest origin influence initial hatchling size and growth potential. Seasonal environmental fluctuations and maternal resource allocation could result in differential hatchling size and development. Hatchlings from ten sites from North Carolina to Florida representing 2 subpopulations were sampled during 3 phases of the season. The largest (WT, SCL and SCW) hatchlings came from the northernmost site with initial size decreasing as latitude decreased. Turtles deposited during the earliest phase of the nesting season grew faster than those from later phases of the season. Differences in initial size and growth potential could influence early stage survivorship as a function of size-based predation, and may imply the need for separate consideration when constructing population models.

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INTRODUCTION

Sea turtles are large, migratory reptiles with complex life histories and long life expectancies. Long-lived organisms such as sea turtles generally exhibit high adult survivorship, iteroparity, and delayed sexual maturity (Janzen et al. 2000, Heppell et al. 1999). Iteroparity in the loggerhead sea turtle (*Caretta caretta* L.) involves multiple discrete breeding events throughout a nesting season, and requires females to partition and allocate limited resources across this period.

Natural selection will favor reproductive and life history strategies that maximize lifetime reproductive success (Haenel and John-Alder 2002). Sea turtles have large adult body size, yet lay multiple clutches of many small eggs relative to their body size when compared with other aquatic turtles (Wilbur and Morin 1988, Van Buskirk and Crowder 1994). This reproductive strategy spreads the allocation of reproductive effort across many eggs and hatchlings, stages with high risk of mortality (Van Buskirk and Crowder 1994).

The adult body size of an individual is the result multiple factors including its initial size at hatching, growth rate, resource quality, age at maturity, and adult growth rates (Congdon and van Loben Sels 1991). An animal's body size has profound significance to its structure and function (Schmidt-Nielsen 1984), representing a tradeoff between the costs and benefits associated with resource allocation. Larger body size reduces early stage predation risk (Davenport and Scott 1993a) and increases total fecundity in adult females. Populations of loggerheads with larger females produce larger eggs and larger hatchlings (Van Buskirk and Crowder 1994). However, there is an

energetic cost associated with locomotion and migration in aquatic animals, as energy must be consumed in order to overcome drag while swimming (Vogel 1983). With other factors equal, larger animals swimming at the surface may have a greater cost of transport since they experience greater drag (Prange 1976). Therefore, a tradeoff must exist between the anatomical constraints (defined by mass, volume, shape and phylogeny) and the potential advantages of a large body size that determines the optimum size of the animal (Schmidt-Nielsen 1984).

Hatchling vulnerability to predators is often size dependent, as many avian and piscine predators are gape limited (Lawrence 1958, Stein and Magnuson 1976, Zaret 1986, Rice et al. 1993). Larger hatchlings may be more difficult to capture and/or swallow than their smaller counterparts (Bustard 1979, Swingland and Coe 1979, Janzen 1993). Janzen (et al. 2000) predicted another benefit of larger size: improved locomotor performance. For hatchlings that migrate through predator-rich shallow water, faster locomotion reduces exposure time to predators (Janzen et al. 2000). In sea turtles, selection may favor consistently high growth rates to a large size to reduce the risk of predation (Davenport and Scott 1993a). However, higher growth rates are likely to increase food intake requirements, so this potential advantage may be reduced in food-limited environments. From these predictions, I hypothesize that growth rate may directly affect survival during the critical early-stage period when survival odds are low.

Because growth profoundly affects the fundamental aspects of an animal's ecology (e.g. duration at each size class and those associated risks), analysis of growth variation as a function of ecology may yield useful insights into the selection pressures shaping life history patterns (Wilbur 1975, Dunham and Gibbons 1990, Bolten et al.

1992). Inherent in the complex life history cycle is flexibility in the duration of each stage, determined primarily by growth rate. This study systematically examined how time of nest deposition and latitude are correlated with initial size and subsequent growth.

The Western North Atlantic loggerhead population can be genetically separated into two large nesting subpopulations; the Northern (extending from North Carolina to northeast FL ~ 29°N), and the southern Florida subpopulation (extending from ~ 29°N on the east coast to Sarasota), and three small subpopulations (FL panhandle, Dry Tortugas and the Yucatan peninsula, Bowen et al. 1993, Bowen 1995, Encalada et al. 1998). Genetic and nest environmental differences between the hatchlings from northern and southern subpopulations of loggerheads (Encalada et al. 1998) may be correlated with differences in their size at emergence or different growth potentials. Interregional differences in size-specific growth and mean adult size have been found in limited growth-interval data for some stocks of green turtles and loggerheads (Limpus 1992; Green 1993; Bjorndal and Bolten 1988; Chaloupka and Musick 1997), but little is known of growth patterns at the earliest ontogenetic stages. Population models used to manage species or subpopulations rely on accurate early estimates of life stage survival patterns to evaluate or predict patterns at later stages. It is important to empirically determine whether hatchlings from the northern and southern subpopulations enter the ocean at similar sizes, and consequently are exposed to the same age/size-based mortality risks.

OBJECTIVES

My objectives were to investigate growth rates of neonate loggerhead hatchlings (*Caretta caretta* L.). Four key questions were addressed:

- (i) Are there differences in the initial size of hatchlings emerging from nests at different times and at different geographical locations?
- (ii) Are there differences in the growth rates of hatchlings sampled at different times throughout the nesting season?
- (iii) Are there differences in growth rates of hatchlings sampled from sites in the northern latitudes (North Carolina, South Carolina, and Georgia)?
- (iv) Are there differences in the growth rates of hatchlings sampled from sites in the southern latitudes (southeast Florida)?

MATERIALS AND METHODS:

Experimental Design

Most growth studies use absolute growth rates, where growth is described as a change in size measured in length or weight recorded over time (Chaloupka and Musick 1997). Biologists most often use two fundamental quantities that can be accurately measured: mass and linear dimension (Schmidt-Nielsen 1984). For this study, mass and the linear dimensions of straight carapace length (SCL) and width (SCW) were used as measures of growth. Body depth (BD) was also considered as an indicator of body condition.

The same individuals were measured in a captive setting for up to 9 weeks. Absolute growth was described as a measure of g/d or mm/d averaged over the duration

of the study as illustrated by the following equations, where T_1 represents the date of initial measurement and T_2 represents the date of final measurement:

$$\text{Growth Rate (g/d)} = [(\text{Mass}_{T_2}) - (\text{Mass}_{T_1})] / (T_2 - T_1)$$

$$\text{Growth Rate (mm/d)} = [(\text{Length}_{T_2}) - (\text{Length}_{T_1})] / (T_2 - T_1)$$

Properly maintained captive hatchlings grow rapidly, but most biologists agree that captive growth rates do not represent wild growth rates (Swingle et al. 1993, Chaloupka and Musick 1997). Captive growth rates are 2-3 times faster than in turtles housed in semi-natural captive conditions (Uchida 1967, Frazer and Schwartz 1984, Chaloupka and Musick 1997). Variation in growth is most likely due to genetic effects when environmental variation is controlled (Haenel and John-Alder 2002). I documented captive growth rates under controlled conditions, and examined the range of variation among individuals that was not due to environmental variation. I made no attempt to compare captive growth with wild growth, for reasons cited above.

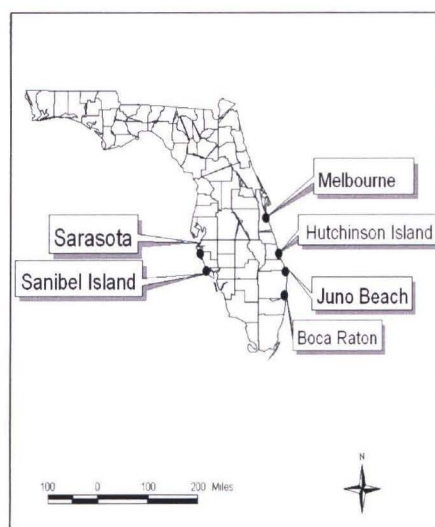
Study Sites and Collection Times in Florida

I selected study sites (Fig. 1) from index nesting beaches (FMRI 2002), each with sufficient historical data to characterize nesting patterns. These sites represented natural beaches (not renourished within the last 5 years). Hatchlings were collected using standard methods prior to or during emergence (Wyneken and Salmon 1992).

In most cases, 10 hatchlings were taken from each of 4 nests at each beach during the beginning, middle and end of the nesting season. Actual sample sizes per beach

varied slightly as indicated below, resulting in a total sample population of 450 hatchlings. The phases of the nesting season were determined by dividing typical nesting periods into thirds based on recent historical records of nest incubation duration and nest densities. The sampling periods in Florida were “Early” (May 11th to June 7th), “Middle” (June 10th to July 10th) and “Late” (July 19th to July 27th). The sample population included hatchlings representing the northern, middle, and southern nesting ranges of Florida. The sites sampled were Melbourne Beach (n = 110 hatchlings, 11 nests), Hutchinson Island (n = 110 hatchlings, 11 nests), Juno Beach (n = 110 hatchlings, 11 nests) and Boca Raton (n = 120 hatchlings, 12 nests). Hatchlings were also collected from sites on the southwest coast of Florida at Sanibel Island (n = 60 hatchlings, 6 nests) and Sarasota (n = 120 hatchlings, 12 nests).

Fig. 1. Location of the hatchling collection sites (Melbourne, Hutchinson Island, Juno Beach, Boca Raton, Sarasota and Sanibel Island) sampled on the southeast and southwest coasts of Florida.

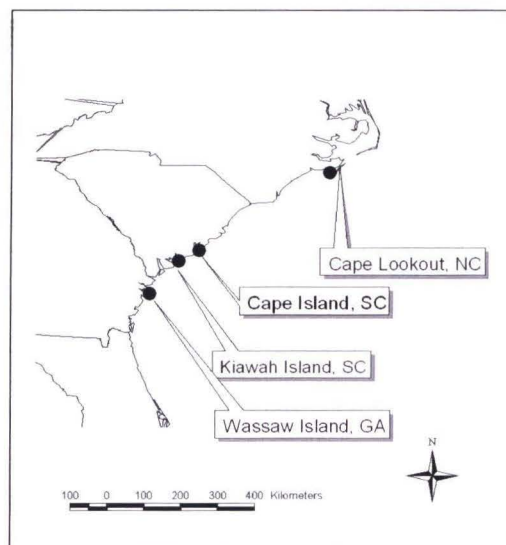


Study Sites and Collection Times for the Northern Subpopulation

A total of 490 hatchlings was collected from sites (Fig. 2) in North Carolina at Cape Lookout (n = 90 hatchlings, 9 nests), South Carolina at Kiawah Island (n = 110 hatchlings, 11 nests) and Cape Island (n = 130 hatchlings, 13 nests), and Georgia at Wassaw Island (n = 160 hatchlings, 16 nests).

Differences in nesting densities, nesting season duration and weather produce a nesting density distribution that differed slightly from that in the south. Efforts were made to sample all parts of this distribution: Georgia Early (laid between May 16th and June 3rd), Middle (June 6th to June 25th) and Late (July 9th to July 20th); South Carolina Early (May 24th to May 31st), Middle (June 8th to June 10th), and Late (July 13th to July 18th); and North Carolina Early (June 9th to June 12th), Middle (June 11th to June 28th) and Late (July 30th). My goal to sample 10 hatchlings from each of 4 nests during the early, middle and late parts of the season in North Carolina, two beaches in South Carolina and Georgia was nearly attained.

Fig. 2. Location of the hatchling collection sites for the northern subpopulation in North Carolina (Cape Lookout), South Carolina (Cape Island and Kiawah Island) and Georgia (Wassaw Island).



Hatchlings

Hatchlings were transported from their home beaches to the holding facility in Styrofoam[®] coolers on moist sand within 48 h of their emergence. Hatchlings from Melbourne Beach were occasionally held in 10-gallon aquaria with seawater for up to 48 h before transport. Turtles were photographed and marked at the beginning of the study to identify individuals. Florida hatchlings were raised at the Gumbo Limbo Environmental Complex/Florida Atlantic University Marine Laboratory (n = 450) whereas northern hatchlings were raised at the Duke University Marine Laboratory (n = 490). After the 9 wk study, East Coast posthatchlings were released offshore into the Gulfstream while West Coast turtles were released in the Florida Loop Current or southwestern extent of the Florida Current.

Housing conditions

Upon arrival, the hatchlings were inspected and placed in quarantine for 3-5 d until they began eating. The turtles were housed in polyethylene pools equipped with flow-through seawater and maintained at $27^{\circ}\text{C} \pm 2^{\circ}\text{C}$ using submersible heaters to approximate thermal conditions in the Gulfstream. Natural spectrum Verilux[®] fluorescent lighting (200-700nm, 6000K, 12L: 12D) was provided from 122 cm double bulb fixtures hung 76 cm above the water surface. Each hatchling was maintained singly within a 20 cm x 20 cm plastic mesh basket with flow-through sides and a solid bottom, facilitating adequate water exchange and providing a feeding platform. The mesh sides also provided for a 3-dimensionally visually complex environment, allowing for visual field diversity thought to be necessary for proper neurological development in other

vertebrates (Hubel and Wiesel 1962, Knudsen 2002). The baskets were secured by floating PVC racks that standardized inside water column depth at 15 cm. Debris was removed from the bottom of the pool and the baskets daily. Complete water changes were done no less than once weekly, and baskets and pools were scrubbed as needed using 2% Novasan[®]. Any turtle exhibiting health problems (soft carapaces and reduced appetites) was removed from the growth study, and treated using antibiotics and dietary change (Choromanski et al. 1987; Appendix A, Table A1).

Feeding and Nutrition

The hatchlings were fed peeled bait shrimp (*Pennaeus spp.*) once daily, supplemented with Mazuri[®] Amphibian and Carnivorous Reptile Gel diet once weekly. Pelagic loggerhead hatchlings are considered opportunistic omnivores, consuming the animals living within the *Sargassum* community, insects blown offshore, and *Sargassum spp.* stipes and floats (Witherington 2002). Gut content analyses of stranded wild post-hatchling turtles confirmed the presence of shrimp and *Sargassum* as primary in the natural diet (Alexander 2000). However, *Sargassum* was not offered in this study.

Each individual received 20% of its body weight in food over the initial 2-wk period to allow them to feed *ad libitum*. The hatchlings started eating within 4-5 d, and consumed most or all of the food offered by the end of two weeks. After Week 2, they were fed 8% of their body weight daily to provide an amount that balanced the project goals of optimal growth with long-term health. Turtles were housed and fed individually to prevent feeding hierarchies so that individual growth potentials could be maximized (Rajagopalan 1984).

Measurements

Mass to the nearest 0.01 g was measured using an electronic balance (Ohaus[®] Model TS400D), and lengths (SCL, SCW and BD) were measured weekly with Vernier calipers to the nearest 0.05 mm. An average of 3 BD measurements was used for this metric to reduce error resulting from lung expansion.

Statistical analysis

Growth rates (g/d and mm/d) were analyzed using a single clutch average from 10 individuals to provide one independent experimental unit per clutch with clutches from the same beach serving as replicates. To determine if the data sets were normally distributed, normality was confirmed using the Kolmogorov-Smirnov test (Dytham 1999). If normal, differences among the sample groups were analyzed using a univariate Two-way Analysis of Variance (ANOVA) with replication to test the null hypothesis of equal treatment effects from “Beach” and “Season” factors (Winer et. al 1991). *Post hoc* pairwise comparisons were conducted using Tukey HSD Tests (Winer et. al 1991). Levene’s Test of Equality of Error Variance (Winer et. al 1991) was used to confirm homogeneity of variance. When data showed significant differences in variance, non-parametric (Kruskal-Wallis) tests were used to identify differences among the groups, and Mann-Whitney *U* Tests were used for pairwise comparisons (Dytham 1999). An α level of 0.05 was considered significant for all statistical tests.

The northern sample was raised under experimental conditions as similar as possible to the Florida sample population. However, because of slight differences between the rearing conditions across facilities, growth data were analyzed separately.

Early and Middle phase hatchlings were compared for a 9-wk duration. Because fall water temperatures could not be maintained within the $\pm 2^{\circ}\text{C}$ range at the end of the study, the Late season turtle measurements were not used past Week 5 in Florida. Data from turtles reared at the Duke University Marine Laboratory were analyzed for a 7-wk period when water temperatures were maintained within the required range. Initial measurements from southwest Florida turtles were included in the initial size comparisons, but differences in their rearing conditions excluded them from comparisons with the other sites. Hence, the growth studies compared only Atlantic Coast representatives of the two subpopulations.

RESULTS

Initial size comparisons

Measurements taken within 48 h of emergence revealed that turtles from the northern subpopulation were larger in every measure during every phase of the nesting season (Tables 1-3). Levene's Tests of Equality of Error Variances were not significant for initial WT, but were significant for the SCL ($p < 0.001$) and SCW ($p = 0.011$). Two-way ANOVA comparisons (Table A2) among the sites (North, Southeast Florida and Southwest Florida) showed that Beach influenced initial hatching weight ($F_{9, 82} = 8.14$, $p < 0.001$). Cape Lookout, NC produced significantly heavier hatchlings (Tukey HSD *post hoc* tests, $p < 0.001$) than all other beaches. Cape Island, SC produced the second largest turtles. Both the Cape Lookout and Cape Island turtles were significantly heavier than the lightest hatchlings at Melbourne Beach (Tukey HSD *post hoc* tests, $p = 0.013$) and Sanibel Island (Tukey HSD *post hoc* tests, $p = 0.019$), Florida.

Initial SCL and SCW differed significantly (Kruskal-Wallis, $\chi^2_{(2)} = 19.13$, $p < 0.001$) among sites (Northern, Southeast FL, and Southwest FL). Cape Lookout produced the longest and widest hatchlings, while the shortest and narrowest hatchlings came from Juno Beach (Tables 1-3). Pairwise comparisons revealed no significant differences among the linear dimensions between Southeast and Southwest Florida turtles. However, there were significant differences in the SCL ($U = 276.50$, $p = 0.020$) and SCW ($U = 273.00$, $p = 0.017$) between the Northern and Southwest Florida hatchlings, and between the Northern and Southeast Florida turtles (SCL, $U = 538.00$, $p < 0.001$; SCW, $U = 630.50$, $p < 0.001$).

Table 1. Average initial measurements of loggerhead hatchlings in southeast Florida from Boca Raton (BR), Hutchinson Island (HI), Juno Beach (JU) and Melbourne Beach (ME) in the 2002 nesting season.

LOCATION	INITIAL WT (g)	SD	INITIAL SCL (mm)	SD	INITIAL SCW (mm)	SD	# OF NESTS
BR Early	19.96	2.07	44.72	0.62	34.30	1.69	n=4
BR Mid	18.84	2.13	44.23	1.44	33.25	1.14	n=4
BR Late	17.13	1.51	43.82	1.02	33.38	1.08	n=4
AVG BR	18.64	1.90	44.26	1.03	33.64	1.30	n=12
HI Early	19.29	1.52	44.48	1.29	33.66	0.51	n=4
HI Mid	19.60	0.90	45.45	1.12	34.77	1.79	n=4
HI Late	16.97	1.59	43.40	2.15	33.45	1.35	n=3
AVG HI	18.62	1.34	44.44	1.52	33.96	1.22	n=11
JU Early	18.85	2.11	43.91	1.34	33.10	2.29	n=4
JU Mid	18.28	1.26	43.97	1.18	33.74	1.18	n=4
JU Late	18.88	1.60	44.83	1.09	34.74	0.78	n=3
AVG JU	18.67	1.66	44.24	1.20	33.86	1.42	n=11
ME Early	18.17	1.42	44.55	1.60	34.85	1.54	n=4
ME Mid	17.44	0.74	44.41	0.71	35.02	0.72	n=4
ME Late	18.63	0.81	45.70	1.19	35.42	0.80	n=3
AVG ME	18.08	0.99	44.89	1.17	35.10	1.02	n=11
Avg SE FL	18.50	1.47	44.46	1.23	34.14	1.24	n=45

Table 2. Initial measurements of loggerhead hatchlings in southwest Florida from Sarasota (SA) and Sanibel Island (SN) in the 2002 nesting season.

LOCATION	INITIAL WT (g)	SD	INITIAL SCL (mm)	SD	INITIAL SCW (mm)	SD	# OF NESTS
SA Early	19.38	2.95	45.63	1.77	34.13	1.61	n=4
SA Mid	19.25	1.32	44.88	1.87	34.28	1.72	n=4
SA Late	19.05	2.04	43.95	0.89	32.73	1.41	n=4
AVG SA	19.23	2.10	44.82	1.51	33.71	1.58	n=12
SN Early	15.30	0.00	43.00	0.00	33.60	0.00	n=1
SN Mid	18.10	0.75	44.57	0.74	34.80	0.52	n=3
SN Late	19.70	0.00	46.30	0.00	36.10	0.00	n=2
AVG SN	17.70	0.75	44.62	0.74	34.83	0.52	n=6
AVG SW FL	18.46	1.77	44.72	1.32	34.27	1.58	n=18

Table 3. Initial measurements of loggerhead hatchlings in the northern subpopulation from Cape Lookout, NC (LO), Cape Island, SC (CI), Kiawah Island, SC (KI), and Wassaw Island, GA (WI) in the 2002 nesting season.

LOCATION	INITIAL WT (g)	SD	INITIAL SCL (mm)	SD	INITIAL SCW (mm)	SD	# OF NESTS
WI Early	18.73	1.90	44.02	2.91	35.03	2.31	n=4
WI Mid	19.82	1.27	46.22	1.18	34.94	1.46	n=8
WI Late	18.87	1.95	45.60	1.09	35.14	1.28	n=4
AVG WI	19.14	1.71	45.28	1.73	35.04	1.68	n=16
LO Early	25.98	3.91	50.76	2.67	40.77	3.21	n=3
LO Mid	21.03	1.30	47.36	0.59	37.04	0.81	n=4
LO Late	25.38	2.60	49.93	1.63	39.51	2.49	n=2
AVG LO	24.13	2.60	49.35	1.63	39.11	2.17	n=9
CI Early	19.80	1.22	45.03	1.08	34.97	1.11	n=4
CI Mid	19.76	1.03	45.81	0.64	34.75	1.14	n=5
CI Late	20.08	2.02	45.78	1.71	35.72	0.94	n=4
AVG CI	19.88	1.42	45.54	1.14	35.15	1.06	n=13
KI Early	19.02	1.00	45.18	0.67	33.95	0.62	n=4
KI Mid	19.83	1.03	45.37	1.63	35.24	1.25	n=4
KI Late	18.80	2.11	45.03	1.61	34.93	1.06	n=3
AVG KI	19.22	1.38	45.19	1.30	34.71	0.98	n=11
Avg North	20.38	1.78	46.24	1.45	35.76	1.47	n=49

Growth rates in southeast Florida over 5 weeks

There were no significant differences in the daily weight gains among hatchlings from the different sites in southeast Florida during different phases of the nesting season (Appendix A, Table A3). There was a significant downward trend in the linear growth rates (SCL, SCW and BD) as the season progressed (Fig. 3). Season was responsible for significant overall declines in SCL, (ANOVA $F_{2,30} = 11.62$, $p < 0.001$), and SCW (ANOVA $F_{2,30} = 13.66$, $p < 0.001$). These differences occur between the Early and Late phases (Tukey HSD, $p < 0.001$) and between the Middle and Late phases (Tukey HSD, $p < 0.001$), with the slowest growth seen in the Late phase. BD measures differed in variance (Levene's Test, $p = 0.004$), so Kruskal-Wallis Tests were used. There was a significant difference associated with Seasons ($\chi^2_{(2)} = 17.53$, $p < 0.001$), but not the Beaches. Pairwise comparisons by the Mann-Whitney U Test revealed significant differences between the Early and Late season nests ($U = 24.00$, $p < 0.001$), and between the Middle and the Late season nests ($U = 9.50$, $p < 0.001$).

Growth rates in Florida over 9 weeks

Growth rates were faster among turtles from Early season nests than turtles from Middle season nests (Figure 4, ANOVA $F_{1, 22} = 8.31$, $p = 0.009$). There were no significant differences among the Beaches (Appendix A, Table A4). Seasonal differences were also apparent between these turtles in SCL ($F_{1, 22} = 6.64$, $p = 0.017$), SCW ($F_{1, 22} = 5.35$, $p = 0.031$) and BD ($F_{1, 22} = 5.02$, $p = 0.036$). A summary of the weekly measurements is found in Appendix A, Tables A5-A8.

Fig. 3. A 5-wk comparison of neonate SCL, SCW and BD growth rates (mm/d) between beaches in southeast Florida in the Early, Middle and Late phase of the nesting season. (Shaded bars show means, error bars 95% CI, and significant differences are indicated by brackets).

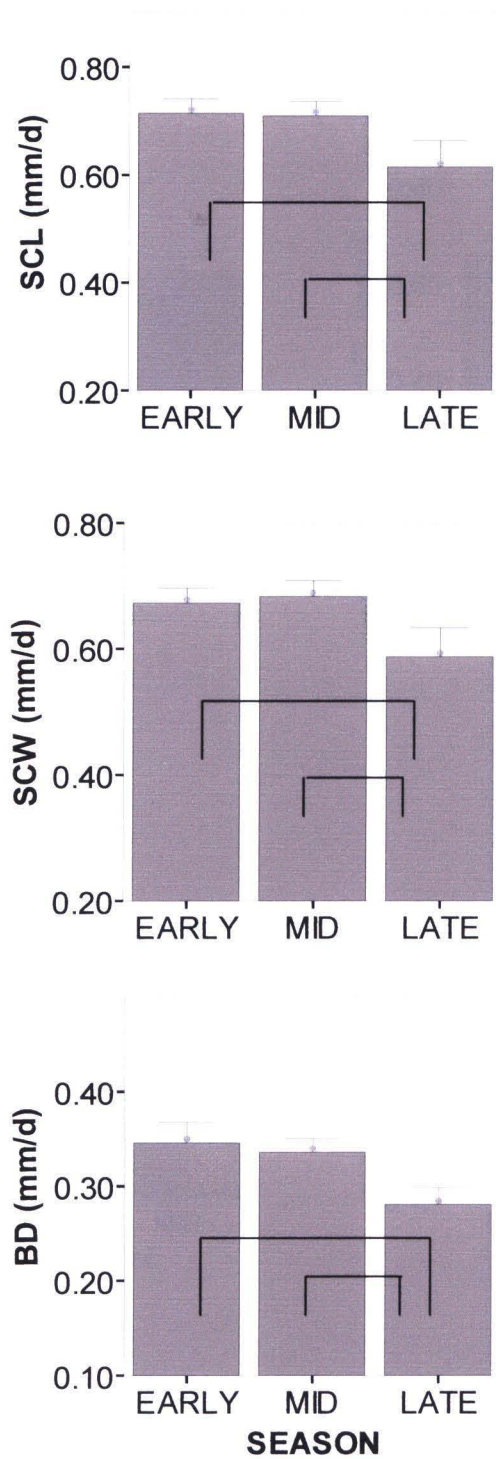
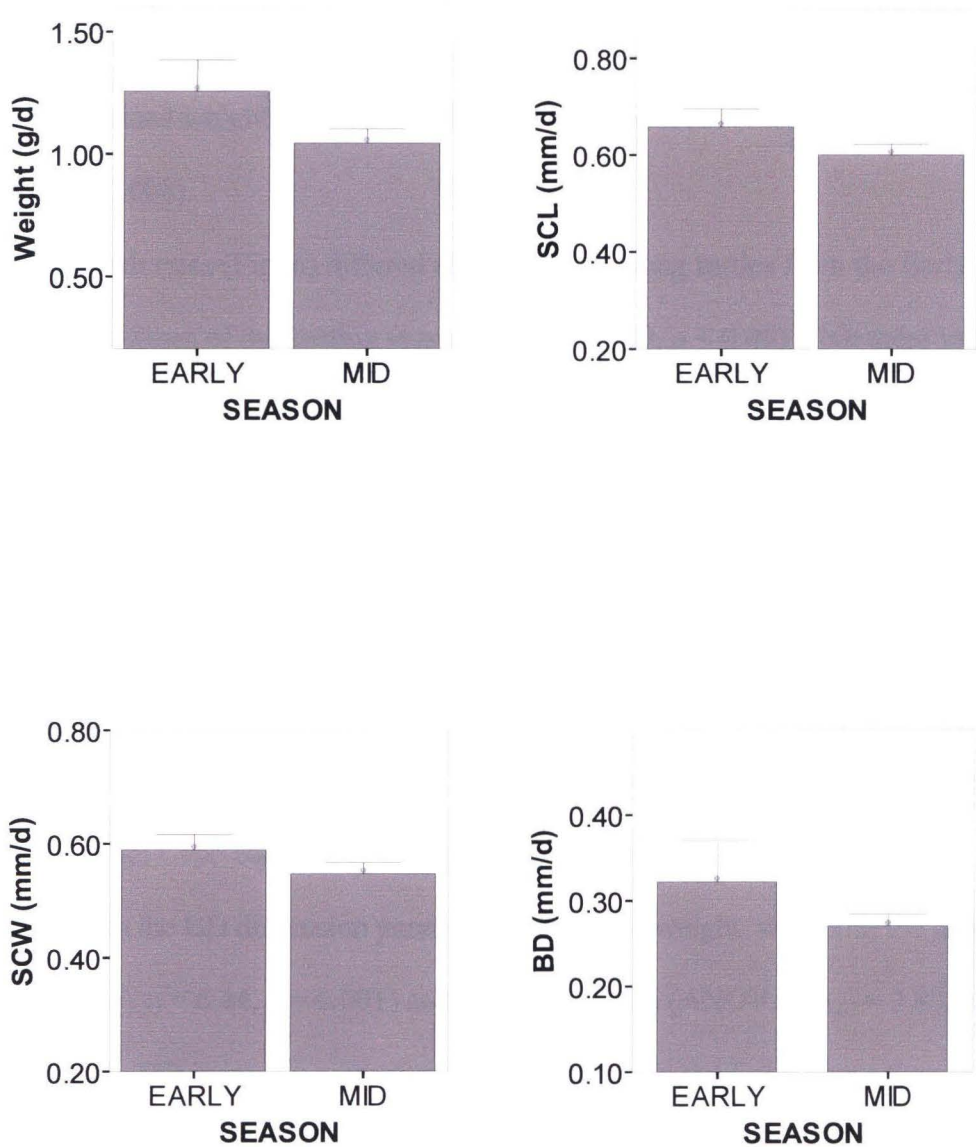


Fig. 4. A 9-wk comparison of neonate weight gains (g/d), SCL, SCW and BD growth (mm/d) between beaches in southeast Florida in the Early and Middle phases of the 2002 nesting season. (Shaded bars show means, error bars show 95% CI).



Growth rates in the northern subpopulation over 7 weeks

There were significant differences in hatchling weight gain (Fig. 5) as a function of season ($F_{2,37} = 3.76, p = 0.033$) as well as beach site ($F_{3,37} = 3.89, p = 0.016$, see Appendix A, Table A9). Weight gain in Early season hatchlings was more rapid than those of Late season hatchlings (Tukey test, $p = 0.009$). Cape Lookout, NC produced hatchlings that gained weight significantly faster than those from Wassaw Island, GA (Tukey test, $p = 0.008$).

SCL growth rates (Fig. 6) differed significantly among turtles from the Early, Middle and Late phases of the nesting season ($F_{2,37} = 10.80, p < 0.001$), but there were no Beach effects. The differences occurred between the Early and Middle season hatchlings (Tukey HSD test, $p = 0.011$), and the Early and Late season hatchlings ($p < 0.001$) with early season hatchlings exhibiting the fastest growth rates.

The SCW growth rates followed a different pattern (Fig. 7). The beach site proved significant (ANOVA $F_{3,37} = 12.31, p < 0.001$), while the phase of the nesting season did not. The hatchlings from Cape Lookout, NC had faster SCW growth rates than the turtles from Cape Island, SC, Kiawah Island, SC and Wassaw Island, GA.

Changes in the BD dimension paralleled changes in weight, with both the nesting beach (ANOVA $F_{3,33} = 6.44, p = 0.001$) and phase of season (ANOVA $F_{2,33} = 3.83, p = 0.032$) significant. BD increases were significantly greater in the Early phase than the Middle phase (Tukey test, $p = 0.021$) and the Late phase (Tukey test, $p = 0.008$). Cape Lookout produced significantly larger ($p < 0.001$) hatchlings than Wassaw Island.

Although inferential statistics were not used to compare growth rates between the northern and southern subpopulation because of the potential for differences in rearing

conditions, some general comparisons can be drawn. Daily growth rates were greater for all measures (weight, SCL and SCW) in the northern turtles at every beach and across all phases of the nesting season. However, these northern turtles were larger initially, and when proportional growth increases were compared, the increases were almost identical in the two subpopulations (197% increase in weight and 57-59% increase in SCL over a 5-wk period). A summary of the weekly measurements is found in Appendix A, Tables A10-A13.

Fig. 5. A 7-wk comparison of neonate weight gains (g/d) and BD (mm/d) among beaches representing the northern subpopulation in the Early, Middle and Late phases of the 2002 nesting season. (Shaded bars show means, error bars show 95% CI).

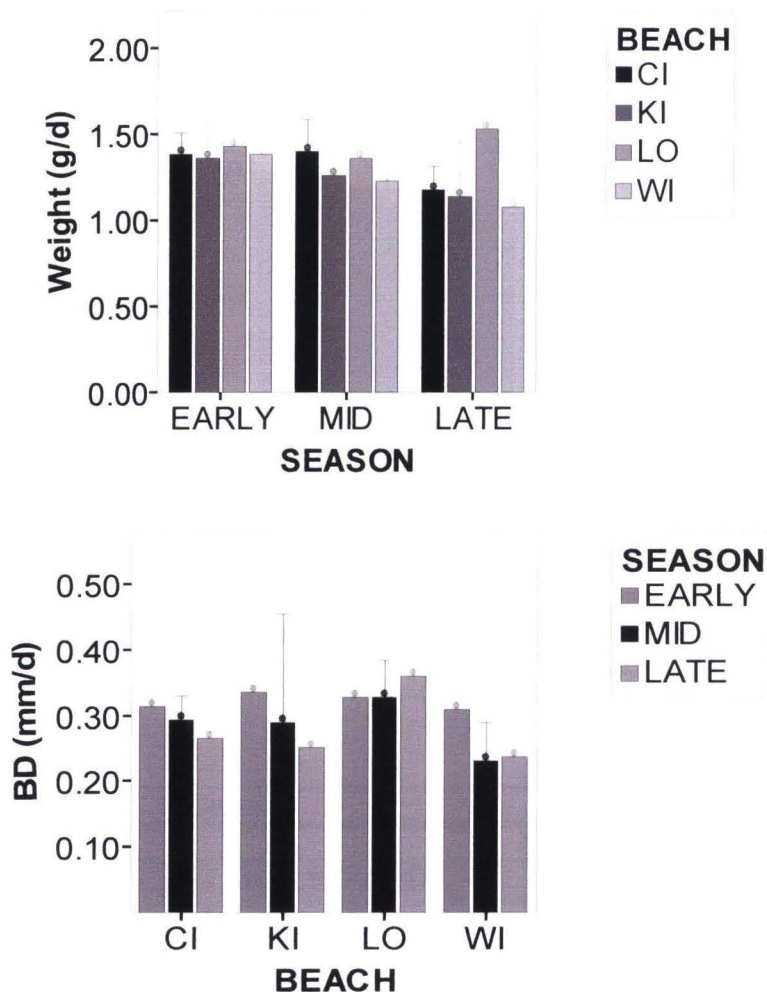


Fig. 6. A 7-wk comparison of neonate growth rates in SCL and SCW compared among beaches representing the northern subpopulation in the Early, Middle and Late phases of the 2002 nesting season. (Shaded bars show means, error bars 95% CI, and significant differences are indicated by brackets).

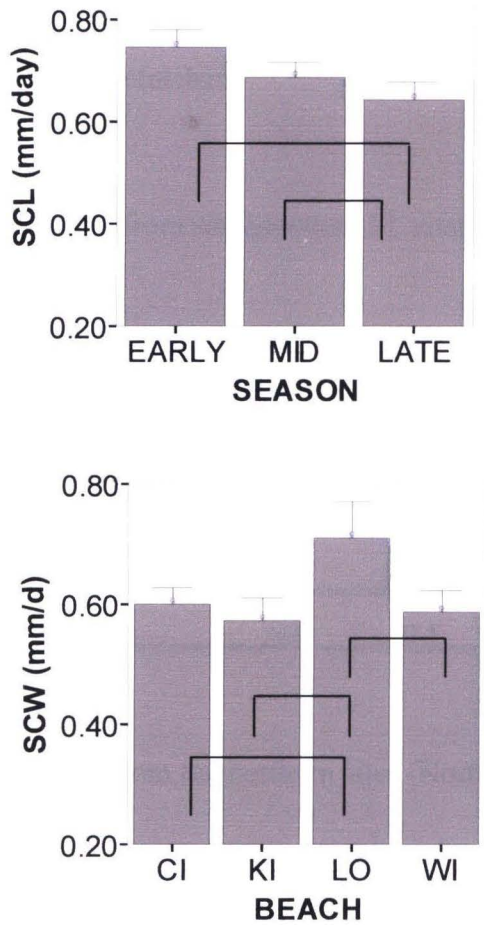


Table 4. A summary of the main results of all analyses. Significant factors (Beach and Season) are indicated for each measurement parameter (WT, SCL, SCW, and BD).

Analysis	Beach	Season
Initial	WT, SCL, SCW, BD	n.s.
5-WK FL	n.s.	SCL, SCW, BD
9-WK FL	n.s.	WT, SCL, SCW, BD
7-WK North	WT, SCW, BD	WT, SCL, BD

Reproductive Effort

There were more eggs per clutch in the northern nests than in the nests from southeast Florida (Tables 5-7). Results from my study, however, do not identify statistically important differences in the total number of eggs from each study site because of high variance among clutches.

Table 5. Nesting data summary from southwestern FL sites.

Southwest Florida Nesting Data Summary					
Location	Incubation Duration Range (Mean)	Average # of eggs	Emergence Success (%)	Date Laid	# of Nests
Avg SA Early	53-61 (59.3)	91	66.3	5/20-5/29	n=4
Avg SA Mid	48-59 (52.7)	124	56.3	6/18-6/20	n=4
Avg SA Late	46-50 (48.7)	106	34.3	7/19-7/27	n=4
Avg SN Total	48-62 (56.4)	97	75.2	6/5-7/24	n=6
Avg SW FL	53.80	103	62.1		

Table 6. Nesting data summary from the northern sites (North Carolina, South Carolina and Georgia).

NC, SC and GA Nesting Data Summary					
Location	Incubation Duration Range (mean)	Average # of eggs	Emergence Success (%)	Date Laid	# of nests
Avg WI Early	51-64 (57.3)	105	87.8	5/16-6/3	n=4
Avg WI Mid	49-56 (53.0)	109	58.0	6/10-6/26	n=6
Avg WI Late	48-57 (54.0)	110	59.0	7/6-7/20	n=4
Avg LO Early	60-63 (61.3)	106	92.7	6/9-6/12	n=3
Avg LO Mid	52-55 (54.0)	115	87.5	6/22-6/25	n=4
Avg LO Late	58-61 (58.0)	135	87.4	6/28-7/30	n=2
Avg CI Early	54-58 (59.3)	115	85.1	5/27-5/31	n=4
Avg CI Mid	54-58 (56.4)	119	89.6	6/8-6/10	n=5
Avg CI Late	50-53 (51.3)	109	81.5	7/13-7/18	n=4
Avg KI Early	57-59 (58.0)	106	62.4	5/24-5/27	n=4
Avg KI Mid	52-58 (55.8)	104	85.6	6/8-6/10	n=4
Avg KI Late	50-55 (52.3)	113	83.2	7/17/03	n=3
Avg North	56.2	106	80.0		

Table 7. Nesting data summary from southeastern FL sites.

Southeast Florida Nesting Data Summary					
Location	Incubation Duration Range (mean)	Average # of eggs	Emergence Success (%)	Date Laid	# of Nests
Avg BR Early	53-60 (55.8)	127	71.5	5/17-6/7	n=4
Avg BR Mid	55-57 (56.0)	93	87.2	6/10-6/12	n=4
Avg BR Late	45-52 (48.0)	86	48.9	7/22-7/26	n=4
Avg HI Early	54-60 (57.3)	93	62.2	5/16-5/31	n=4
Avg HI Mid	53-64 (58.0)	103	75.0	6/13-6/20	n=4
Avg HI Late	48-53 (50.0)	102	64.9	7/26-8/1	n=3
Avg JU Early	56-58 (56.8)	104	78.0	5/15	n=66*
Avg JU Mid	54-56 (55.0)	68	87.2	6/15	n=3
Avg JU Late	47-48 (47.3)	103	90.5	8/1-8/2	n=3
Avg ME Early	60-63 (61.5)	126	84.7	5/11-5/24	n=4
Avg ME Mid	56-62 (59.3)	96	61.1	6/11-6/12	n=4
Avg ME Late	50-52 (51.0)	72	68.8	7/26-7/27	n=3
Avg SE FL	54.0	98	73.3		

* beach average used

DISCUSSION

The ecological importance of body size in sea turtles is apparent at each life history stage; size influences hatchling survivorship, juvenile recruitment, duration of size specific mortality risks, and in sexually mature females, fecundity. While knowledge of the selective advantage of phenotypic variation is a crucial primary step in understanding of the evolution of life history traits (Sinervo and Doughty 1996), few data are available to address this. Measurements of phenotypic variation are often based on field studies and cannot control for multiple effects on phenotypes.

Growth studies such as this one strive to identify the proximate causal mechanisms and patterns of phenotypic variation in growth rates. The ability to succeed in multiple habitats, each with stage-specific risks of mortality, often involves maximizing physiological and morphological performance to minimize mortality risks.

The factors that ultimately determine an individual's body size represent a balance between resource acquisition and allocation and the energetic costs associated with each.

Evolution of rapid growth rates could result from selection on body size through size-specific mortality risk (Sinervo et al. 1992). It has been theorized that the life history of sea turtles necessitates rapid growth to minimize size-specific mortality risk (Davenport and Scott 1993a). In addition, although all long-lived turtles (such as sea turtles) mature relatively late, those with the highest growth rates mature earlier than those with slower growth rates (Congdon et al. 1993). Hence, the larger hatchlings from the northern nests may mature more quickly than hatchlings from other sites.

Initial Body Size at Hatching

An individual's size at hatching has important consequences for its later survival, growth and reproductive success (Roff 1992, Sinervo 1993, Sinervo and Doughty 1996). Lack (1954) noted that for groups with no parental care (such as sea turtles), selection should favor a compromise between the quantity and quality (size) of offspring (Sinervo et al. 1992). Selection for large offspring will be balanced by selection on the number of offspring (Lack 1954, Williams 1966, Smith and Fretwell 1974).

Phenotypic plasticity in the size of loggerheads at hatching extends beyond genetics to include the impact of the incubation environment (Ackerman 1997, Glen et al. 2003). How an embryo adapts to a particular environment involves a potential range of phenotypes, or the "reaction norm," expressed by an inherited genotype across a range of environmental conditions (Gilbert 2003). The hydric and thermal properties of the nest have consequences on initial hatchling size. Cooler nest temperatures were generally

associated with higher humidity and longer incubation periods (Packard 1999, Reece et al. 2002). Hatchling size correlates with the amount of water available to facilitate optimal yolk metabolism in a number of turtle species, including sea turtles (Morris et al. 1983, Miller and Packard 1992, Packard et al. 1993, Packard 1999, Reece et al. 2002). Rates of embryonic growth and yolk consumption in snapping turtles (*Chelydra serpentina* L.) are directly related to the water reserve contained within the egg (Morris et al. 1983, Packard et al. 1982, Packard and Packard 1984). Eggs in a drier environment hatched sooner and produced smaller hatchlings than those in wetter environments, suggesting that embryos in different hydric environments have different metabolic rates (Morris et al. 1983, Packard and Packard 1984). In an analysis of loggerhead hatchlings from natural nests, temperature correlated negatively and percent water content correlated positively with hatchling carapace length (Reece et al. 2002). A study of green sea turtles produced similar results, where hatchlings experiencing warmer incubation temperatures were significantly smaller, suggesting that temperature may play an important part determining phenotypic variation in hatchlings (Glen et al. 2003).

At the study sites in Florida, monthly rainfall amounts (9.6-33.3 cm) peaked during the 2002 nesting season and average daily air temperatures ranged between 25.5°C and 29°C (Florida Climate Center, NOAA archives 2002). Monthly rainfall averages were similar at the Cape Lookout site (14.0-31.2 cm), and slightly lower along the coasts of South Carolina (5.6-19.1 cm) and Georgia (5.3-12.7 cm) during the incubation period of the nesting season (Weather Services International, NOAA archives 2002). However, average daily air temperatures were generally several degrees cooler (20-26.5°C) in North and South Carolina than at Florida beaches (Weather Services

International, NOAA archives 2002), possibly increasing nest humidity depending on the water potential of the substrate.

In this study, the largest hatchlings (WT, SCL and SCW) came from Cape Lookout, NC, the northernmost site in the sample. Mean nest incubation temperatures were slightly cooler here ($29.2^{\circ}\text{C} \pm 1.7$) than at the other beaches in the northern sample (Cape Island $30.1^{\circ}\text{C} \pm 2.2$; Kiawah Island $29.6^{\circ}\text{C} \pm 1.9$; Wassaw Island $29.6^{\circ}\text{C} \pm 2.3$), supporting the negative correlation between incubation temperature and hatchling carapace length reported in other studies.

The smallest turtles were found, as expected, in Florida. In general, initial weights followed a gradient down the coast, with the heaviest turtles found farthest north (highest latitudes) and lightest ones found farthest south (lowest latitudes). Mean nest incubation temperatures generally increased as latitude decreased (Melbourne Beach 27.7°C , SD = 1.9; Hutchinson Island 29.8°C , SD = 1.1; Juno Beach 30.7°C , SD = 1.1; Boca Raton 30.3°C , SD = 1.2). The same pattern of decreasing size with decreasing latitude was displayed by the SCL measurements, where Cape Lookout produced the longest turtles, followed by turtles in South Carolina, Georgia and Florida.

Incubation temperature and humidity alone may not be responsible for hatchling size from the northern and southern ends of the nesting range. Differential maternal resource allocation may be implicated, however there are no data from sea turtles to support this hypothesis. Egg weight, diameter and lipid content were not considered in this study, and, therefore, cannot be included in my analysis. In theory, differences in nesting season duration could impact temporal resource allocation between nesting females in different regions. Since northern hatchlings leave the nesting beaches larger

and heavier, they may be less susceptible to size dependent predation and mortality than their southern counterparts.

Whether the larger initial size of these hatchlings will increase their overall survival, however, is uncertain. Though larger hatchlings may have stronger locomotor skills as they enter the water and escape predators more effectively (Miller et al. 1987, Janzen 1993, Packard 1999), they may have consumed more yolk and need to locate food sooner than smaller hatchlings with larger yolk reserves (Reece et al. 2002). There may also be increased energetic costs of transport for the larger hatchlings (Schmidt-Nielsen 1972) necessitating increased food intake requirements. The average initial hatchling sizes in this study ranged between 17.2-26.0 g (WT) and 43.6-50.8 mm (SCL), so the smallest turtles were about 50% lighter and 20% shorter than the largest hatchlings. It is likely, though, that risk of size dependent predation greatly outweighs risk of starvation due to depleted yolk reserves and cost of transport, and that the larger hatchlings are most likely better adapted for survival in the offshore migration.

Reproductive Effort

Loggerheads lay an average of 112 eggs every 14 days, with a clutch frequency of 3-4 nests/year and a remigration interval of 2-4 years (Hirth 1980, Dodd 1988, Van Buskirk and Crowder 1994). Reports indicate that turtles from the northern subpopulation tend to lay fewer nests with more eggs (Richardson and Richardson 1995, Cordes and Rikard 2002, Van Buskirk and Crowder 1994). For example, loggerheads nesting at Little Cumberland have a lower than average reported clutch frequency of 2.5 nests/year, with a larger than average clutch size of 120 eggs (Richardson and Richardson

1995). It is possible that females in the northern part of the nesting range are partitioning nesting resources differently than the Florida turtles because of differences in the length of the nesting season.

Hatchling growth rates

Normal or optimal growth and development directly affect the hatchlings' capacities to forage effectively and avoid predation. Hatchlings that reach a larger size more quickly are less vulnerable to predation and may possess a survival advantage. This study was the first to systematically address temporal and spatial variables that affect growth rates in other species of reptiles.

Most reptilian growth studies report wide variability in individual growth rates, even when environmental conditions are closely controlled, indicating that genetic variation in growth rates among individuals may be common (Andrews 1982, Sinervo et al. 1992). Previous studies with green turtles have found that growth is extremely variable among individuals. However, individual growth rates are stable, indicating that each turtle may have a "preprogrammed" maximum growth rate determined by genetics (Davenport and Scott 1993b). However, subjects in the Davenport and Scott study were housed collectively and fed to satiation, increasing the possibility that larger turtles fed disproportionately. Larger turtles may have also inhibited the growth of the smaller turtles, thereby exaggerating variability (Davenport and Scott 1993b, Davenport and Oxford 1984, Davenport et al. 1989). My study eliminated these variables as turtles were individually housed and feeding amounts were controlled, allowing me to investigate differences in growth rates strictly on the basis of temporal and spatial origin.

The ability of individual hatchlings to maximize their growth potential may impact their locomotor performance. Larger and/or stronger turtles may be more likely to successfully “run the gauntlet” from the surf zone to the protection of the offshore nursery areas faster than smaller turtles. In a study involving another long-lived turtle (*Trachemys scripta elegans*), larger body size at hatching was significantly correlated with improved survival (Janzen et al. 2000). These data suggest that all else being equal (including the composition of predator populations in both regions), individual hatchlings from the northern subpopulation may potentially have a survival advantage over their smaller southern subpopulation conspecifics.

Seasonal Growth Component

One aim of this study was to analyze the growth rates of hatchlings from the beginning, middle and end of the nesting cycle to determine if there were differences in seasonal growth potential between the clutches. Theoretically, resources may be allocated differently by females during different phases of the nesting season, due to seasonal variation in energy reserves, food availability/quality during vitellogenesis and/or other energy demands limiting the energy budget. Seasonal environmental fluctuations in the nest environment during the incubation period may also affect the growth and development of the hatchlings. The loggerhead data presented here show that growth rates are fastest in the Early phase turtles regardless of the beach, latitude or subpopulation. Consequently, these hatchlings may be more likely to survive their offshore migration than hatchlings from later in the season.

Growth rates in Florida over 5 weeks

Independent of the initial weight at hatching, turtles coming from 4 beaches on the southeast coast of Florida throughout the entire nesting season had a similar potential to increase mass in the first 5 weeks of life. There was a slight reduction in the growth rates from the Early sample group to the Late sample group in all 4 measurement parameters. Turtles from the beginning of the nesting season grew longer and developed a deeper body depth profile than those at the middle or end of the nesting season. Carapaces grew significantly wider in turtles from the beginning and middle of the season than at the end.

In captive growth studies, since the turtles experience similar energetic costs, growth is more directly influenced by the quality and quantity of food and by water temperature (Nuitja and Uchida 1982). Since food quality and amount stayed consistent throughout this study, slightly lower water temperatures and temperature fluctuations ($\pm 2^{\circ}\text{C}$), in addition to genetic differences and maternal effects, are the likely causes for differences in growth rates late in the season. Although water temperatures throughout the study stayed within a narrow range previously shown not to affect growth rates in other reptile species (Sinervo et al. 1992), the differences may have been enough to cause a slight decline in growth rates over this relatively short study. Temperatures in the Gulfstream where loggerhead hatchlings spend their first several months to years, remain relatively constant near $26\text{-}27^{\circ}\text{C}$ (NOAA Satellite Active Archive 2002). Hatchlings leaving the coast of Florida experience relatively constant sea surface temperatures as they swim to the Gulfstream throughout the season (NOAA Satellite Active Archive 2002), dropping off only slightly ($\sim 2\text{-}3^{\circ}\text{C}$) towards the end of the season.

Although not investigated in this study, it is theoretically possible that females were utilizing the majority of their resources at the beginning and middle of the season, producing hatchlings with a greater capacity for survival when environmental conditions (such as hydric content, temperature and/or beach stability) are generally most favorable. Those eggs laid at the end of the nesting season may be of lower quality, as the nests are more likely to be lost to late summer tropical storms, erosion, and fluctuations in the incubation environment. Successful hatchlings may emerge less robust due to tidal inundation.

Growth rates in Florida during a 9-wk period

Growth rates over a 9-wk period were significantly lower for turtles from the Middle part of the nesting season than the Early phase in all measurement parameters. As expected, variation increased as a function of time in the 9-wk analyses. Individual variation is high in growth studies (Andrews 1982, Sinervo et al. 1992, Davenport and Scott 1993a), and is likely amplified as sampling duration increases. The beach from which the hatchlings came did not affect their overall growth rates, and it is likely that in southeast Florida, the nesting beaches are not sufficiently separate geographically to influence growth rates. Regional climate ($< 2^{\circ}\text{C}$ average air temperature differences) (Florida Climate Center, NOAA archives 2002) and environmental conditions within the nest may not differ dramatically within the ~250 km separating the northern-most and southernmost beaches in this study. It appears hatchlings from across the southeast Florida nesting range exhibit similar growth potential, likely due to similarities in their incubation environments.

Another important experimental factor to consider is the effect of the holding basket on growth rate as the turtles age. In fish, for example, growth rates decrease when container space is limited (Weatherley 1972). Growth curves (Appendix B, Figures A1-A4) indicate a shift from increasing linear dimension to increasing weight and a flattening of linear growth curves near the 8-wk point. Whether this inflection represents a true energy partitioning shift from increasing in size (linear dimensions) to increasing storage (weight) is unknown. Further studies are being conducted to elucidate the effects of the holding basket on growth rates. It is also possible that an increase in tank inhabitants as the study progressed may have created some indirect density-induced stress effects, as reported by other large scale rearing operations (Caillouet et al. 1986, Wood 1991), reducing growth rates slightly as well.

Growth rates in the northern subpopulation over 7 weeks

Differences in growth rates between subpopulations living in different latitudes may represent genetically-based adaptations to the environment (Leggett and Carscadden 1978), as selective pressures favor organisms best able to withstand fluctuations within their environment. As well, they may be better equipped for the longer migration to Gulfstream nursery grounds. In the earliest days of the offshore migration, hatchlings leaving beaches in the northernmost boundary of their nesting range are subjected to near shore conditions that may differ considerably from those farther south. Hatchlings leaving northern beaches traverse greater distances (~45-80 km) in colder waters to reach the Gulfstream than do the hatchlings in southeast Florida (~1.5-25 km), potentially increasing exposure time to nearshore predators. Since growth rates in reptiles are

reduced under colder temperatures, it could be expected that hatchlings might not grow as quickly in the colder northern waters as they migrate to the Gulfstream.

It is possible that the northern subpopulation of loggerhead hatchlings could have a greater growth potential as a compensatory factor for the cooler thermal environment. Differential growth is reported in other ectothermic species as a function of latitude. Studies of American shad (*Alosa sapidissima*) show that growth rates are quite uniform within a population, but vary among populations across a latitude gradient (Leggett and Carscadden 1978). Shad from northern rivers were significantly larger in every age class than same-age counterparts in the southern populations in Florida, and the northern subpopulations grew at a faster rate than southern subpopulations (Leggett and Carscadden 1978). Similar genetically-based geographical differences have been demonstrated in populations of king salmon, walleyes, and arctic char (Leggett and Carscadden 1978). It is with less confidence that direct similarities are inferred between long-lived and short-lived ectotherms, however, as their life history strategies differ in many ways.

While a direct comparison of the growth rates between the northern and southeast Florida groups cannot be made here, several general observations can be made. Turtles from every beach representing the northern subpopulation grew substantially faster in all measures and in all phases of the nesting season than turtles from southeastern Florida beaches. The beaches from which the hatchlings came were generally more important in their effect on growth rates in the northern subpopulation than in the south. Significant differences in the growth rates of turtles from different beaches were found in nearly all measurement parameters. Because beaches were spatially more separated (over 565 km)

than in southeastern Florida (~250 km), incubation environments likely differed much more among the northern beaches. Northern turtles from the Early phase of the season grew significantly faster than those in the Middle and Late phases in general, paralleling the trends seen in the southeast Florida turtles.

The larger hatchlings produced at Cape Lookout also grew faster than the rest of the subpopulation sample. From these results, I infer that initial size at hatching has an important relationship to future growth rates. They begin larger, grew faster, and therefore, may be less susceptible to size-dependent predation and more likely to survive. Although these beaches produce fewer turtles, these turtles may be better adapted for their offshore migration to the Gulfstream.

How these differences in growth potential change with time, however, is unclear. It has been suggested that growth rates in the larger size classes (juveniles and subadults) may be greater in loggerheads in the Bahamas and Florida than those turtles in the north, where the northern subpopulation may be disproportionately represented (Medona 1981, Bjorndal and Bolten 1988, Klinger and Musick 1995, Braun-McNeill et al. in press, Heppell 2001). Given the long time to maturity and regional food differences, it is certainly possible to have shifts so that the size trends seen here may be obscured over time. This study focused on the earliest size class and the mortality risks associated therein; consequently predictions regarding survival advantages is limited to this stage.

Applications and Implications

With a better understanding of growth patterns among populations, we can further refine vital rates (time in each life stage, spatially and temporally explicit stage

parameters, and even sex-specific risks of mortality). To formulate effective management plans, we must gain a more thorough understanding of sea turtle growth and population dynamics by correctly estimating demographic rates such as mortality, growth and recruitment rates (Chaloupka and Musick 1997). Further comparative studies of somatic growth, as it relates to sea turtle ecology, will improve our insight into the life history patterns that form the basis for change in populations (Chaloupka and Musick 1997). If northern loggerheads indeed slow their growth rate as they age compared to the southern loggerheads, the northern subpopulation could be slower to recover and affect time to maturity (Braun-McNeill et al. in press).

It is important to understand the duration at each life history stage, including the early-stage pelagic post-hatchlings investigated in this study, as the survival rates at this stage have a large impact on overall population growth (Heppell et al. 2001). Many of the mortality risks at specific stages are anthropogenic, and some are size/stage specific. Of particular concern to this stage are risks associated with sargassum harvest, ingestion of marine debris, and, as they enter larger stages, incidental capture in commercial fishing gear and TED effectiveness (Heppell et al. 2001). Recent studies by Witherington (2002) indicate that 15% of the pelagic post-hatchlings had ingested plastics in the first few weeks after leaving the nesting beach, and 20% had ingested tar. Marine debris tends to accumulate along oceanic current fronts (Carr 1987) and regions of downwelling (Witherington 2002) where pelagic post-hatchlings and juvenile loggerheads occur.

This study provides important empirical data describing morphometric and demographic characteristics of early-stage pelagic post-hatchling loggerheads in the Western Atlantic, partitioning variation in growth potential among key selected factors:

temporal and spatial nest origin, and initial hatch size. Based upon these data, hatchlings from the southern-most and northern-most portions of the nesting range, as well as those from different phases of the nesting season, perhaps should be considered separately when predicting survivorship and total demographic contribution in future population models.

APPENDIX A

Table A1. Ingredients for gelatin diet fed after the growth study.

Ingredients	Amount
Mazuri Aquatic Turtle Pellets	300 g
Marine Fish (e.g. tuna, snapper, etc.)	600 g
Chopped Frozen Spinach	70 g
Unflavored Knox gelatin	225 g (7 boxes)
Water (Heat and divide between pellets and gelatin)	1400 mL
Minerall-I supplement powder	90 g

Table A2. ANOVA summary table for initial weight analyses for northern subpopulation, southwest FL and southeast FL. Statistically significant *p* values indicated by *.

Initial Weights

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Season	2	2.599	1.300	0.438	0.647
Beach	9	217.579	24.175	8.141	<.001*
Season*Beach	18	102.539	5.697	1.918	0.055
Residual	82	243.521	2.970		
Total	111	562.819	5.070		

Table A3. ANOVA summary tables for southeast Florida 5-wk growth rate analyses. Statistically significant *p* values indicated by *.

Weight

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Season	2	0.111	0.056	2.966	0.067
Beach	3	0.052	0.017	0.922	0.442
Season*Beach	6	0.054	0.009	0.484	0.815
Residual	30	0.561	0.019		
Total	41	0.772	0.019		

SCL

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Season	2	0.081	0.040	11.615	<0.001*
Beach	3	0.018	0.006	1.691	0.190
Season*Beach	6	0.016	0.003	0.786	0.588
Residual	30	0.105	0.003		
Total	41	0.217	0.005		

SCW

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Season	2	0.070	0.035	13.659	<0.001*
Beach	3	0.010	0.003	1.356	0.275
Season*Beach	6	0.026	0.043	1.678	0.161
Residual	30	0.077	0.003		
Total	41	0.180	0.004		

FL Early Mid Late 5 Week BD Kruskal-Wallis Test

Source	d.f.	Chi-square	<i>P</i>
Season	2	17.532	<.001*
Beach	3	0.730	0.866

Table A4. ANOVA summary tables for southeast Florida 9-wk growth rate analyses. Statistically significant *p* values indicated by *.

FL Early Mid 9 Week Weight

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Season	1	0.354	0.354	8.305	0.009*
Beach	3	0.059	0.020	0.460	0.713
Season*Beach	3	0.030	0.010	0.234	0.872
Residual	22	0.938	0.043		
Total	29	1.364	0.047		

FL Early Mid 9 Week SCL

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Season	1	0.024	0.024	6.641	0.017*
Beach	3	0.007	0.002	0.647	0.593
Season*Beach	3	0.005	0.002	0.449	0.721
Residual	22	0.080	0.004		
Total	29	0.115	0.004		

FL Early Mid 9 Week SCW

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Season	1	0.012	0.012	5.346	0.031*
Beach	3	0.001	0.000	0.217	0.884
Season*Beach	3	0.004	0.001	0.548	0.655
Residual	22	0.051	0.002		
Total	29	0.068	0.002		

FL Early Mid 9 Week BD

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Season	1	0.021	0.021	5.018	0.036
Beach	3	0.024	0.008	1.889	0.161
Season*Beach	3	0.013	0.004	1.025	0.401
Residual	22	0.094	0.004		
Total	29	2.828	0.098		

Table A5. Summary of the mean weight measurements (g) of hatchlings from Southeast Florida in 2002.

NEST ID	N	INITIAL	WK 1	WK 2	WK 3	WK 4	WK 5	WK 6	WK 7	WK 8	WK 9
BR ¹	40	19.86	26.55	34.44	42.83	51.68	61.33	73.59	84.67	92.96	103.29
HI ¹	40	19.29	22.49	29.42	37.72	45.37	53.24	63.51	73.73	83.83	93.49
JU ¹	40	18.85	23.78	31.37	40.22	47.71	56.13	66.86	78.25	88.70	101.49
ME ¹	40	18.17	23.87	31.29	39.94	47.71	55.27	67.84	79.97	91.44	104.08
BR ²	40	18.84	22.33	29.12	38.25	46.90	52.74	63.30	74.20	76.48	77.65
HI ²	40	19.60	25.81	33.68	43.46	50.95	57.82	69.19	77.87	84.32	87.54
JU ²	40	18.28	22.94	32.18	39.83	45.27	52.83	63.89	67.54	73.95	78.42
ME ²	40	17.44	22.97	31.34	40.50	45.53	55.33	70.97	74.03	82.20	89.34
BR ³	30	17.76	27.58	36.95	41.55	47.22	53.12				
HI ³	30	17.16	27.19	36.41	40.90	45.85	51.59				
JU ³	30	18.45	30.37	38.93	42.20	46.88	53.44				
ME ³	30	18.59	31.92	38.61	46.64	50.70	56.61				

BR=Boca Raton, FL
 HI=Hutchinson Island, FL
 JU=Juno Beach, FL
 ME=Melbourne Beach, FL

¹ Early Season
² Mid Season
³ Late Season

Table A6. Summary of the mean straight carapace length (SCL) measurements (mm) of hatchlings from Southeast Florida in 2002.

NEST ID	N	INITIAL	WK 1	WK 2	WK 3	WK 4	WK 5	WK 6	WK 7	WK 8	WK 9
BR ¹	40	44.72	51.34	57.18	62.83	68.64	73.33	77.91	81.79	84.96	87.56
HI ¹	40	44.48	48.37	53.58	60.47	66.05	70.45	74.82	78.95	82.52	85.76
JU ¹	40	43.91	49.25	55.14	60.69	66.60	71.14	75.48	79.41	83.20	86.54
ME ¹	40	44.55	49.17	54.89	60.85	66.64	71.40	75.96	80.49	84.68	88.84
BR ²	40	44.23	48.24	54.27	61.40	65.90	69.84	74.05	77.93	79.54	80.85
HI ²	40	45.45	50.96	57.06	63.73	68.63	72.81	77.11	80.43	82.81	84.27
JU ²	40	43.97	49.33	55.95	60.91	65.68	70.03	73.70	76.11	78.53	80.21
ME ²	40	44.41	49.45	56.03	62.14	66.24	71.61	76.64	79.69	82.57	84.66
BR ³	30	44.22	53.04	59.35	63.03	66.30	69.40				
HI ³	30	43.60	52.72	58.97	62.80	65.77	68.83				
JU ³	30	44.52	55.20	60.73	63.58	66.31	69.58				
ME ³	30	45.41	55.90	60.93	65.81	68.47	71.72				

BR=Boca Raton, FL
 HI=Hutchinson Island, FL
 JU=Juno Beach, FL
 ME=Melbourne Beach, FL

¹ Early Season
² Mid Season
³ Late Season

Table A7. Summary of the mean straight carapace width (SCW) measurements (mm) of hatchlings from Southeast Florida in 2002.

NEST ID	N	INITIAL	WK 1	WK 2	WK 3	WK 4	WK 5	WK 6	WK 7	WK 8	WK 9
BR ¹	40	34.30	40.60	47.45	52.58	57.43	61.38	65.22	68.58	71.14	73.10
HI ¹	40	33.66	38.57	43.94	49.24	54.29	58.36	61.86	65.39	68.13	70.74
JU ¹	40	33.10	38.81	45.14	50.18	55.41	59.27	62.66	66.31	68.98	71.88
ME ¹	40	34.85	38.97	44.78	50.16	55.01	59.57	63.44	67.08	70.19	73.64
BR ²	40	33.43	37.53	43.94	49.98	55.03	58.76	62.68	65.67	68.20	68.96
HI ²	40	34.77	40.82	46.98	52.97	57.53	61.06	64.39	66.85	69.03	69.81
JU ²	40	33.47	39.46	47.42	52.79	56.58	60.37	63.40	65.60	67.43	68.70
ME ²	40	35.02	40.38	46.40	52.56	56.49	60.66	65.20	67.58	70.00	71.49
BR ³	30	33.27	44.88	50.94	53.54	56.02	58.26				
HI ³	30	33.45	42.96	49.43	52.20	54.24	57.52				
JU ³	30	34.74	45.80	50.73	53.40	55.51	58.08				
ME ³	30	35.42	46.12	50.21	55.24	58.17	60.72				

BR=Boca Raton, FL

HI=Hutchinson Island, FL

JU=Juno Beach, FL

ME=Melbourne Beach, FL

¹ Early Season

² Mid Season

³ Late Season

Table A8. Summary of the mean body depth (BD) measurements (mm) of hatchlings from Southeast Florida in 2002.

NEST ID	N	INITIAL	WK 1	WK 2	WK 3	WK 4	WK 5	WK 6	WK 7	WK 8	WK 9
BR ¹	40	19.59	23.74	26.28	28.49	30.75	32.90	35.05	36.56	37.79	38.51
HI ¹	40	19.89	22.26	24.82	27.48	29.53	31.50	33.52	35.16	36.51	37.92
JU ¹	40	18.14	22.84	25.73	27.64	30.45	32.24	34.54	35.96	37.87	39.60
ME ¹	40	18.17	22.57	25.28	27.05	29.89	31.89	34.34	36.15	38.24	43.77
BR ²	40	19.06	22.22	24.90	27.41	29.93	31.01	32.98	34.54	32.89	34.68
HI ²	40	19.22	23.55	26.13	28.49	30.50	32.04	34.41	35.66	34.04	36.68
JU ²	40	18.66	22.29	25.64	28.04	29.50	31.14	32.82	33.44	32.47	34.62
ME ²	40	17.94	22.11	25.33	27.91	29.00	31.16	34.22	34.82	33.40	36.75
BR ³	30	18.70	24.79	27.48	28.00	29.64	30.20				
HI ³	30	18.29	24.57	27.41	28.32	29.78	30.73				
JU ³	30	19.02	25.25	27.59	27.92	29.52	30.63				
ME ³	30	19.33	25.54	27.52	29.21	29.72	31.12				

BR=Boca Raton, FL

HI=Hutchinson Island, FL

JU=Juno Beach, FL

ME=Melbourne Beach, FL

¹ Early Season

² Mid Season

³ Late Season

Table A9. ANOVA summary tables for NC, SC, and GA 7-wk growth rate analysis. Statistically significant *p* values indicated by *.

Weight

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Season	2	0.182	0.091	3.760	0.033*
Beach	3	0.282	0.094	3.885	0.016*
Season*Beach	6	0.229	0.038	1.579	0.181
Residual	37	0.895	0.024		
Total	48	1.664	0.035		

SCL

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Season	2	0.069	0.034	10.800	<0.001*
Beach	3	0.024	0.008	2.510	0.074
Season*Beach	6	0.032	0.005	1.680	0.154
Residual	37	0.118	0.003		
Total	48	0.257	0.005		

SCW

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Season	2	0.017	0.009	2.879	0.069
Beach	3	0.111	0.004	12.312	<0.001*
Season*Beach	6	0.031	0.005	1.733	0.141
Residual	37	0.111	0.003		
Total	48	0.277	0.006		

BD

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>
Season	2	0.014	0.007	16.010	<0.001*
Beach	3	0.036	0.012	0.515	0.675
Season*Beach	6	0.015	0.003	1.832	0.126
Residual	37	0.061	0.002		
Total	48	3.916	0.082		

Table A10. Summary of the mean weight measurements (g) for the northern subpopulation from Cape Lookout, NC (LO), Cape Island, SC (CI), Kiawah Island, SC (KI), and Wassaw Island, GA (WI) in the 2002 nesting season.

	NEST ID	INITIAL	WEEK 1	WEEK 2	WEEK 3	WEEK 4	WEEK 5	WEEK 6	WEEK 7
EARLY	CI	19.80	21.30	28.55	38.16	48.50	59.46	69.77	82.00
	KI	19.02	22.20	32.52	41.67	50.16	63.23	71.01	85.76
	LO	25.98	34.17	43.25	51.57	62.23	74.23	83.37	94.17
	WI	18.73	22.30	30.26	38.99	48.11	56.85	66.41	78.64
MID	CI	19.76	26.43	36.68	46.70	54.79	65.48	77.95	89.72
	KI	19.83	27.08	35.53	41.62	52.30	60.55	71.29	82.24
	LO	21.03	27.75	37.27	47.95	56.98	65.87	74.07	88.57
	WI	19.82	26.46	33.35	41.54	50.67	60.15	68.90	77.97
LATE	CI	20.08	25.52	34.24	41.61	49.24	56.99	65.90	77.47
	KI	18.80	24.52	32.69	39.47	46.78	54.62	66.23	71.99
	LO	25.38	32.97	43.54	52.18	59.18	68.49	83.53	95.93
	WI	18.87	22.60	29.98	35.37	41.97	48.93	58.16	64.80

Table A11. Summary of the mean straight carapace length (SCL) measurements (mm) for the northern subpopulation from Cape Lookout, NC (LO), Cape Island, SC (CI), Kiawah Island, SC (KI), and Wassaw Island, GA (WI) in the 2002 nesting season.

	NEST ID	INITIAL	WEEK 1	WEEK 2	WEEK 3	WEEK 4	WEEK 5	WEEK 6	WEEK 7
EARLY	CI	45.03	47.04	52.44	59.98	67.14	72.77	77.05	81.66
	KI	45.18	47.12	54.99	61.70	67.29	74.01	77.49	81.89
	LO	50.76	56.62	63.02	68.46	73.86	78.41	82.45	86.33
	WI	44.02	47.91	53.18	59.89	66.08	70.96	75.04	80.16
MID	CI	45.81	51.07	58.89	65.56	69.86	73.97	79.71	83.35
	KI	45.37	50.59	58.00	63.53	68.76	72.97	77.45	81.03
	LO	47.36	52.53	59.43	65.98	71.66	76.35	80.24	84.55
	WI	46.22	51.82	57.71	63.27	68.46	73.29	77.37	80.92
LATE	CI	45.78	50.29	56.24	61.58	66.35	69.83	74.31	77.67
	KI	45.03	49.63	55.84	61.09	65.49	68.98	73.65	77.00
	LO	49.93	54.72	61.54	67.26	71.97	75.79	80.55	84.08
	WI	45.60	49.16	54.72	59.75	62.55	66.49	71.75	75.31

Table A12. Summary of the mean straight carapace width (SCW) measurements (mm) for the northern subpopulation from Cape Lookout, NC (LO), Cape Island, SC (CI), Kiawah Island, SC (KI), and Wassaw Island, GA (WI) in the 2002 nesting season.

	NEST ID	INITIAL	WEEK 1	WEEK 2	WEEK 3	WEEK 4	WEEK 5	WEEK 6	WEEK 7
EARLY	CI	34.97	37.19	42.55	48.44	55.36	59.30	63.12	66.54
	KI	33.95	38.59	43.12	49.90	55.06	59.54	63.61	66.13
	LO	40.77	45.68	51.19	57.47	60.67	64.45	67.43	70.21
	WI	35.03	37.86	43.62	49.15	54.15	58.41	61.75	65.26
MID	CI	34.75	40.79	46.57	53.00	56.82	61.72	65.24	67.78
	KI	35.24	39.65	45.78	51.20	55.87	59.06	62.20	64.87
	LO	37.04	42.05	48.26	54.20	59.77	63.74	67.00	70.00
	WI	34.94	40.91	46.83	51.65	56.50	60.60	63.66	66.17
LATE	CI	35.72	40.28	46.11	51.14	55.29	58.62	61.82	64.70
	KI	34.93	40.32	45.57	50.49	54.43	57.20	61.17	63.34
	LO	39.51	44.79	50.78	55.63	59.92	63.27	66.81	69.44
	WI	35.14	38.58	44.28	48.88	51.45	54.87	59.13	62.18

Table A13. Summary of the mean body depth (BD) measurements (mm) for the northern subpopulation from Cape Lookout, NC (LO), Cape Island, SC (CI), Kiawah Island, SC (KI), and Wassaw Island, GA (WI) in the 2002 nesting season.

	NEST ID	INITIAL	WEEK 1	WEEK 2	WEEK 3	WEEK 4	WEEK 5	WEEK 6	WEEK 7
EARLY	CI	19.50	19.97	22.93	26.99	29.15	31.53	33.02	35.96
	KI	18.94	21.06	23.75	27.56	29.69	31.51	32.50	36.12
	LO	22.22	25.00	27.93	30.30	31.75	33.72	34.92	36.34
	WI	18.62	20.13	22.75	25.89	29.07	30.56	31.07	33.49
MID	CI	20.02	23.90	27.20	29.96	31.50	34.54	34.54	35.99
	KI	19.67	23.33	25.97	27.89	30.50	33.30	32.70	34.85
	LO	20.66	23.03	26.66	28.64	30.09	31.41	32.55	35.06
	WI	20.49	23.22	25.41	27.22	28.7	30.1	31.67	33.11
LATE	CI	19.94	21.93	24.90	26.74	28.50	30.64	33.27	34.41
	KI	19.24	21.39	24.91	25.79	27.75	29.91	32.28	31.75
	LO	22.02	25.27	27.30	30.03	30.23	31.39	34.32	38.17
	WI	19.53	20.86	23.51	24.76	25.59	27.03	29.39	30.29

Figure A1. Growth curves for hatchlings from Boca Raton, FL collected in the Early, Middle and Late phases of the nesting season.

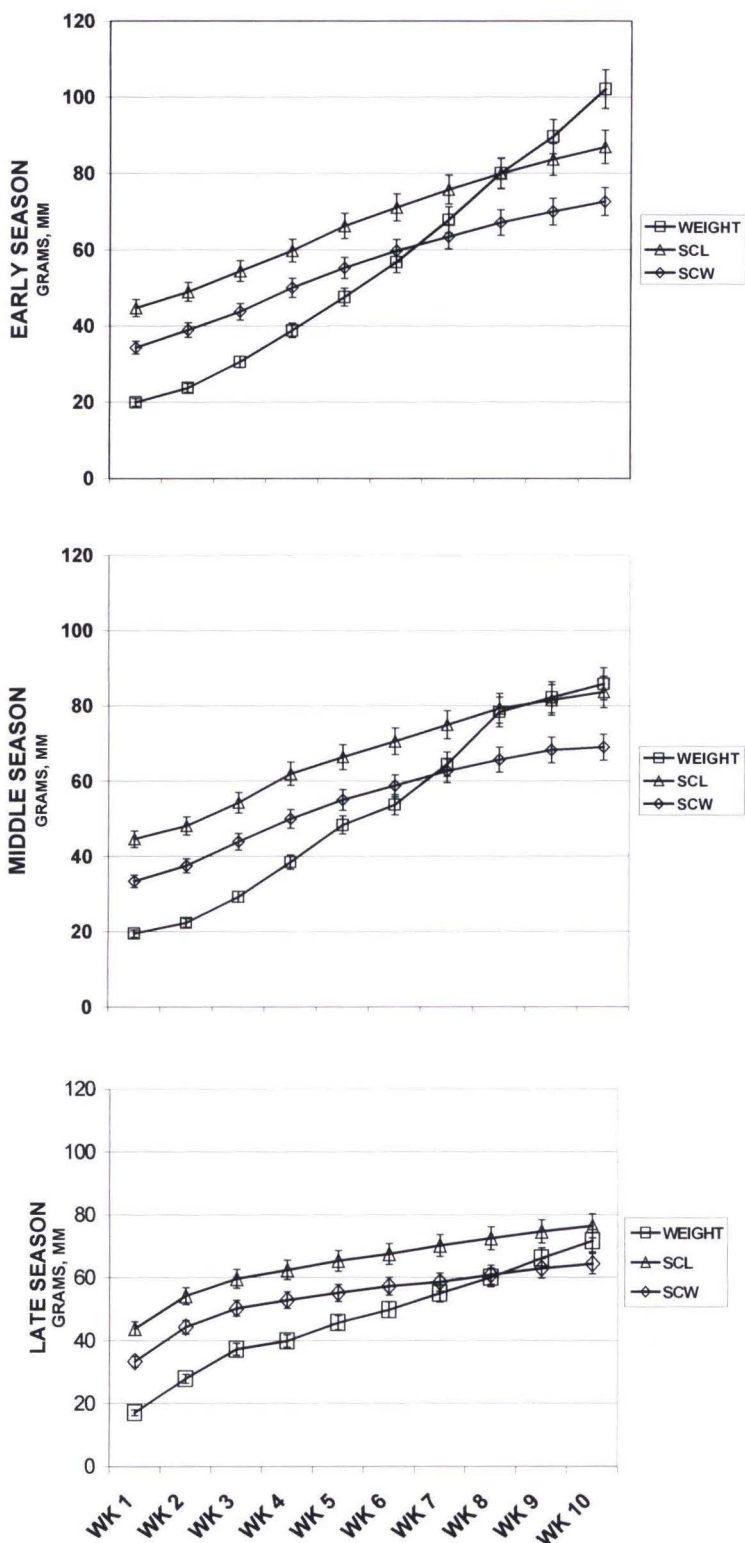


Figure A2. Growth curves for hatchlings from Hutchinson Island, FL collected in the Early, Middle and Late phases of the nesting season.

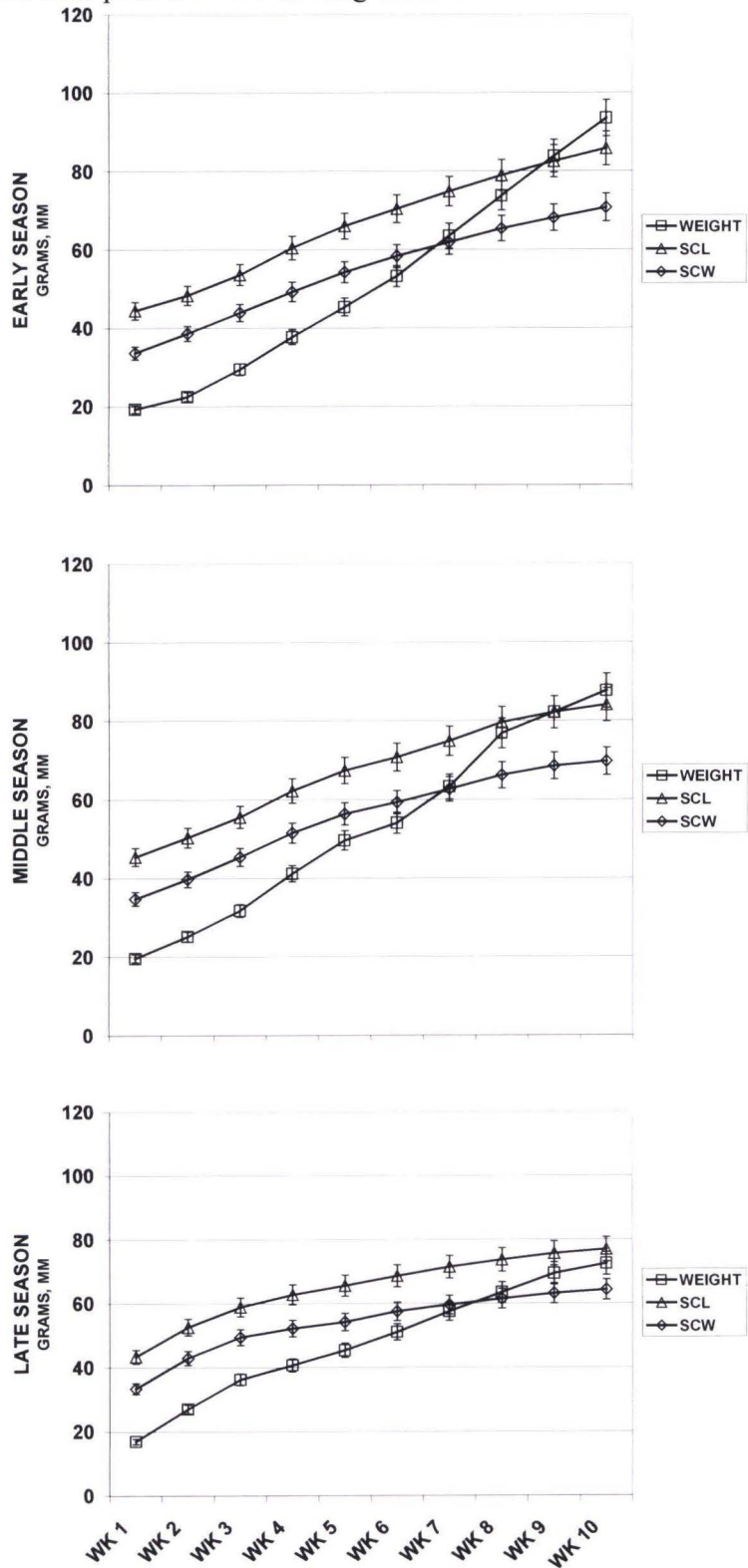


Figure A3. Growth curves for hatchlings from Juno Beach, FL collected in the Early, Middle and Late phases of the nesting season.

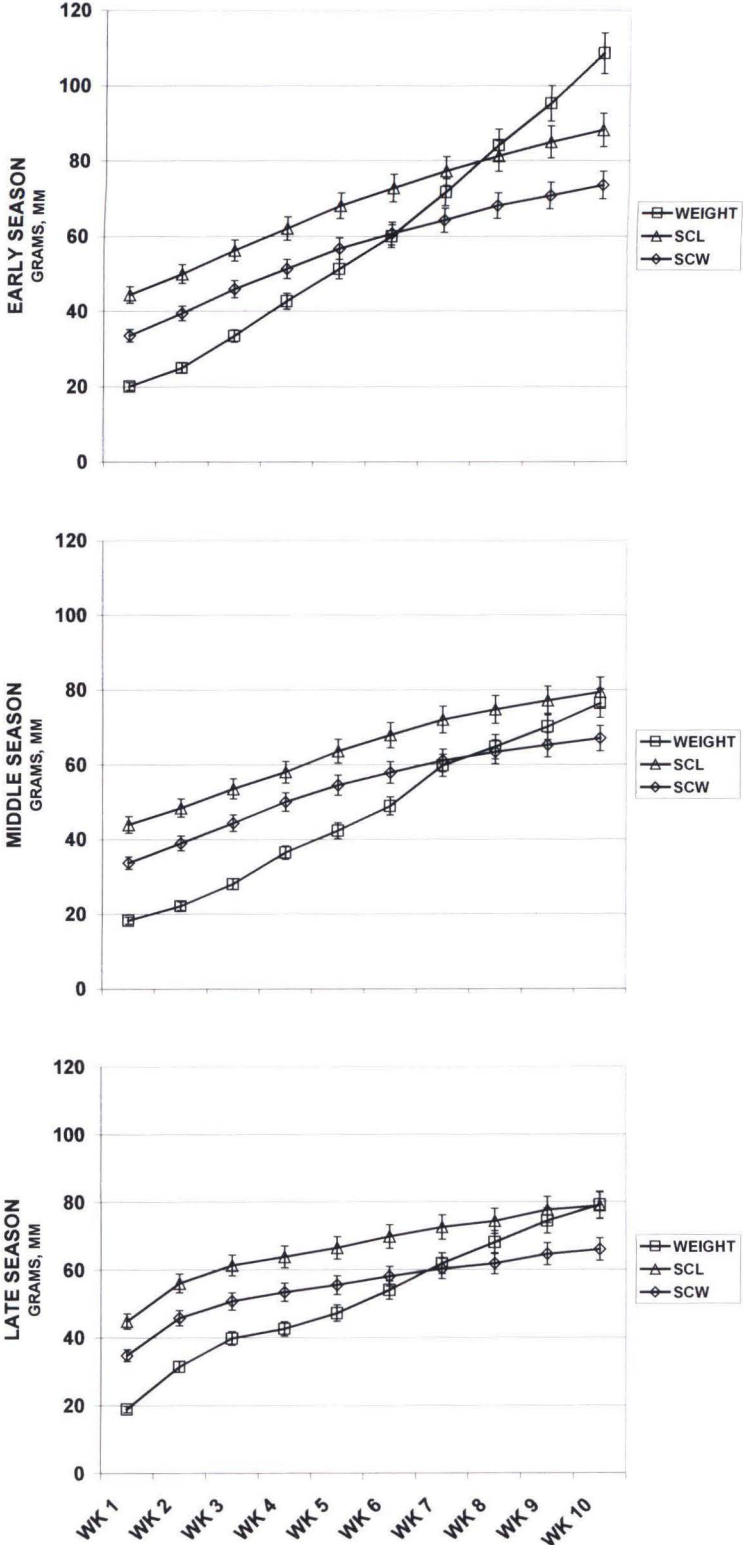
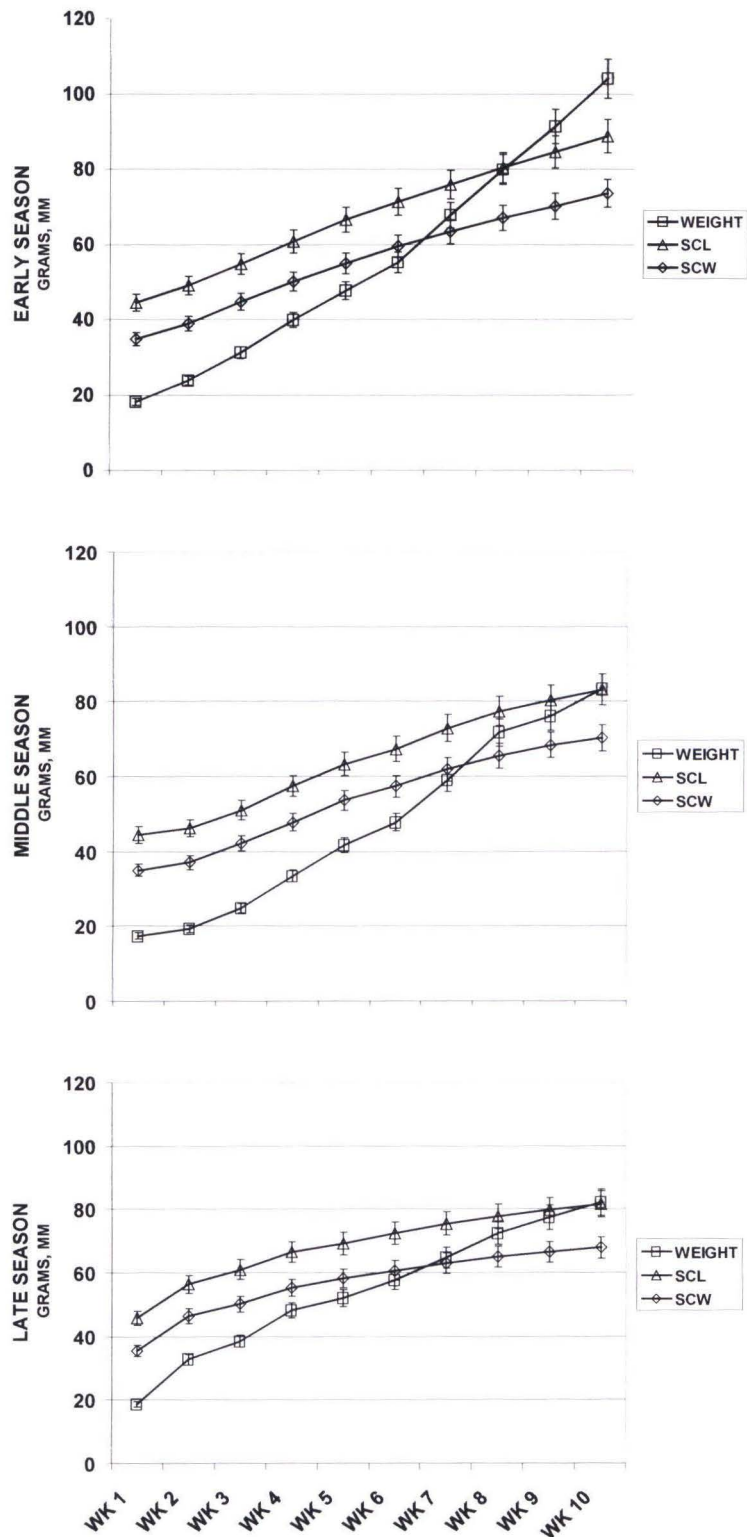


Figure A4. Growth curves for hatchlings from Melbourne Beach, FL collected in the Early, Middle and Late phases of the nesting season.



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