

Growth rates of juvenile green turtles *Chelonia mydas* from three ecologically distinct foraging habitats along the east central coast of Florida, USA

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ABSTRACT: A generalized additive mixed modeling approach was used to assess somatic growth for juvenile green turtles *Chelonia mydas* at 4 sites in 3 ecologically distinct foraging habitats along the east central coast of Florida, USA. The 3 habitats were a man-made nuclear submarine turning basin (Trident Submarine Basin), an estuary (Indian River Lagoon), and oceanic sabellariid worm rock reefs (Sebastian Inlet and St. Lucie Power Plant). Turtles from the Indian River Lagoon site grew significantly faster than turtles from the Trident Submarine Basin and sabellariid worm rock reef sites. There were no significant differences in growth rates between the sabellariid worm rock reef and Trident Submarine Basin sites. Non-monotonic or dome-shaped growth rate functions reflecting an immature peak in growth rates were observed for all 3 habitats. Growth rates peaked in 1998 for turtles in the Trident Submarine Basin and sabellariid worm rock reef habitats; since then growth rates have declined. This temporal decline in growth rates may reflect density-dependent effects on growth as more juveniles recruit to Florida foraging grounds, a direct result of increases in nest production at the primary rookeries (Costa Rica, Florida and Mexico). Developmental habitats are important for the survival of juvenile marine turtles. This study illustrates the degree to which juvenile growth rates vary among developmental habitats, which ultimately can affect the rate of growth and recovery potential of nesting stocks.

KEY WORDS: *Chelonia mydas* · Density-dependent effects · Developmental habitat · Florida · Foraging grounds · Generalized Additive Mixed Model · Green turtles · Growth rate

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INTRODUCTION

The green turtle *Chelonia mydas* is a long-lived, slow-growing marine herbivore that may take as many as 25 to 50 yr to reproduce. Understanding spatial and temporal variability in somatic growth rates is important for understanding the population dynamics of this species (Balazs & Chaloupka 2004, Chaloupka et al. 2004). While recent efforts have focused on variability in individual growth rates and density-dependent effects on green turtle growth (Bjorndal et al. 2000, Chaloupka et al. 2004), little attention has been given to the spatial variability in sea turtle growth behavior (Balazs & Chaloupka 2004, Chaloupka et al. 2004).

Juvenile green turtles recruit to developmental habitats along the US eastern seaboard from Massachusetts in the north to Florida in the south, whereas adult green turtles reside in foraging grounds south of Biscayne Bay, Florida (NMFS & USFWS 1991, Schroeder et al. 2008). The northern extent of the range provides suitable habitat for several species of marine turtles during the warm months (April–October). In the fall, water temperatures decline rapidly and turtles must either move south to warmer coastal waters or east to warmer pelagic waters of the Gulf Stream, or risk exposure to environmental conditions that may ultimately lead to cold-stunning or death (Morreale et al. 1992). The relative abundance of juvenile green turtles

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in the coastal waters of southeast Florida is greatest during the fall and winter months (November–March; Ehrhart et al. 2007), perhaps a result of northern animals moving south and occupying this area. In contrast to the seasonally suitable habitats of the northeastern U.S., juvenile green turtles remain resident in the coastal waters of Florida year-round. Genetic studies (e.g. Bass & Witzell 2000) have indicated that juvenile green turtle foraging aggregations along the east coast of Florida are derived from many nesting stocks, with the greatest contributions coming from Costa Rica, Florida and Mexico. Florida foraging aggregations are therefore directly linked to the growth and recovery of green turtle stocks in the western Atlantic.

Growth rates of wild green turtles have been directly measured for many populations in the western Atlantic using capture-mark-recapture (CMR) studies (Mendonça 1981, Frazer & Ehrhart 1985, Bjørndal & Bolten 1988, Boulon & Frazer 1990, Bolten et al. 1992, Collazo et al. 1992, Shaver 1994, Bjørndal et al. 2000). However, to date, no study in this region has examined the effect of habitat on growth rates of juveniles. Developmental habitats are important for the survival of juvenile marine turtles and the recovery of depleted stocks (Bjørndal et al. 2003). Our objective was to use long-term CMR data sets to model growth rates of juvenile green turtles from 3 ecologically distinct habitats in close geographic proximity along the east central coast of Florida.

MATERIALS AND METHODS

Data set and sampling design. The data set comprised 751 growth records for 497 green turtles captured between 1982 and 2005 at 4 sites in 3 ecologically distinct foraging habitats along 125 km of the east central Florida coast (Fig. 1). The foraging habitats consisted of: (1) a man-made, rock-lined, deepwater basin—the Trident Submarine Basin site, (2) an estuary—the Indian River Lagoon site, and (3) a nearshore oceanic sabellariid worm rock reef complex comprising 2 sites—Sebastian Inlet and St. Lucie Power Plant. All captures were conducted during daylight hours. Turtles were tagged, measured, and released the same day at or near the capture site.

The Trident Submarine Basin is a nuclear submarine turning basin located within the Cape Canaveral Air Station near the mouth of the Port Canaveral Ship Channel (28° 25' N, 80° 35.6' W, Fig. 1). The basin measures approximately 600 by 1200 m. A concrete seawall and wharf forms the eastern side of the basin, and the remaining perimeter is lined with boulders. Water depth increases from 0.5 to 2.5 m along the edges of the basin to approximately 13 m in the center. An algal

mat consisting of *Gelidium americanum*, *Hypnea cervicornis*, *Solieria filiformis*, *Polysiphonia subtilissima*, and *Ulva lactuca* covers the submerged surfaces of the boulders and is the primary food source for juvenile green turtles that feed at this site (Redfoot 1997). Sampling was conducted throughout the year from 1993 to 2005. Large-mesh tangle nets and long-handled, large hoop nets were used to capture turtles.

The Indian River Lagoon system is a complex mosaic of terrestrial, wetland, and estuarine ecosystems that extends 260 km along the east coast of Florida from Ponce de Leon Inlet in the north to Jupiter Inlet in the south. It consists of 3 lagoons: the Mosquito Lagoon, the Banana River, and the Indian River Lagoon—a shallow brackish water estuary. Turtles were captured at a site in the Indian River Lagoon located approximately 65 km south of Cape Canaveral and 3 km south of Sebastian Inlet on the west side of the barrier island (27° 49' N, 80° 26' W, Fig. 1). Seagrass beds composed of *Syringodium filiforme* and *Halodule wrightii* are found in shallow waters (<1 m); however, it is the large beds of drift algae (*Bryothamnion seaforthii* and *Graciliaria* spp.) that serve as the primary food source for juvenile green turtles (Holloway-Adkins 2001). Turtles were captured year-round from 1982 to 2005 using large-mesh tangle nets.

Nearshore sabellariid worm rock reefs are found in Florida from Cape Canaveral to Biscayne Bay and are formed by polychaete worms *Phragmatopoma laticosta* (Kirtley & Tanner 1968, Main & Nelson 1988). The reef structures extend from the intertidal zone to a depth of approximately 10 m. This type of reef is substrate for at least 109 species of benthic marine algae (Juett et al. 1976), but only some are consumed by juvenile green turtles (Holloway-Adkins 2001, Gilbert 2005). Growth data from 2 sites, Sebastian Inlet and St. Lucie Power Plant, along this reef complex were included in the present study. The Sebastian Inlet Reef site is east of the Indian River Lagoon site, separated only by a narrow stretch of barrier island (27° 49' N, 80° 25' W, Fig. 1). Rough ocean conditions during much of the year prevent safe access to the reefs; therefore, turtles were captured only during the calmer summer months from 1989 to 2005 using a large-mesh tangle net. The St. Lucie Power Plant Reef site is located approximately 60 km to the south on Hutchinson Island (27° 21' N, 80° 14' W, Fig. 1). The power plant draws cooling water from the Atlantic Ocean through 3 large diameter pipes (3.9 to 4.9 m) into a 1500 m long intake canal. The structures housing the intake pipes are 365 m offshore in about 7 m of water. Turtles encountering these structures are often transported into the intake canal where they are captured with tangle nets, large hoop nets, or by divers. The benthic environment near the intake structures consists pri-

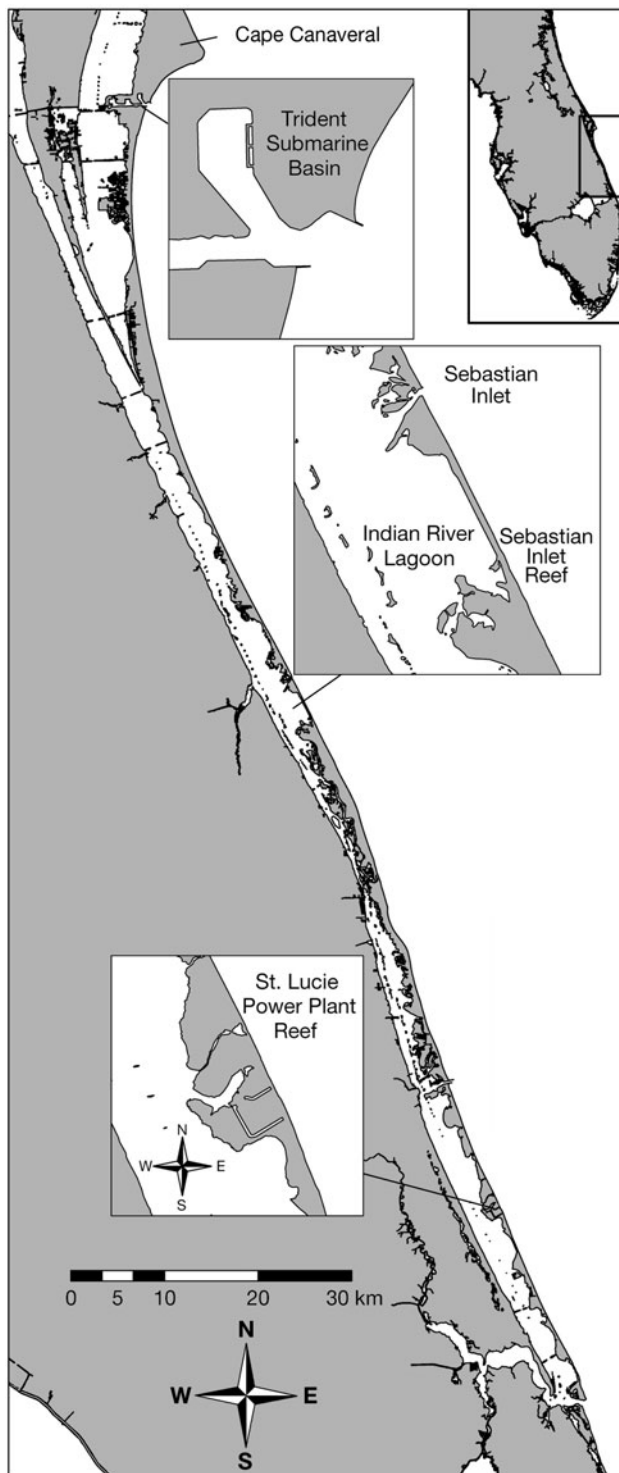


Fig. 1. Study sites along the east central coast of Florida: Trident Submarine Basin, Indian River Lagoon, Sebastian Inlet Reef, and St. Lucie Power Plant Reef

marily of sand and shell sediments (ABI 1991), although sabellariid worm rock reefs lie just to the southwest (<450 m). Sampling was conducted 5 to 7 d

a week throughout the year. Data from 1991 to 2003 were used for the present study. The 2 reef sites were considered as distinct sites because tag recoveries indicated that movement of turtles between these sites was minimal and the foraging aggregations were indeed different groups of turtles.

Each turtle was tagged with external flipper tags, either Monel or Inconel metal tags or plastic roto-tags that were applied to the second proximal scale of both front flippers. Passive integrated transponder (PIT) tags were used in addition to external flipper tags beginning in 1993 at the Trident Submarine Basin and in 1996 at the Indian River Lagoon and Sebastian Inlet Reef sites. One PIT tag was inserted into the right front flipper near the shoulder of each turtle. PIT tags were not used at the St. Lucie Power Plant site.

Straight carapace length (SCL) was measured for each turtle from the nuchal notch to the posterior-most point of the carapace using calipers accurate to 0.1 cm. Carapace injuries and abnormalities were noted and measurements for turtles with injuries affecting SCL were not included in the present study. All turtles were visually examined for the presence of fibropapilloma tumors and assigned a score based on the severity of the disease (Work & Balazs 1999).

Capture history profiles were constructed for each recaptured turtle. Profiles included: (1) capture dates, (2) SCL at each capture, (3) time at large (mo) since first capture or previous recapture, and (4) annual growth rate. To minimize the potential bias from seasonal effects on growth rate, only growth values resulting from capture intervals greater than 10 mo were included in the analysis. Recapture intervals included in the present study ranged from 10 mo to 7.6 yr, with the median recapture interval for each foraging ground ranging from 1.3 to 1.9 yr. A summary of the number of captures and sampling period is given for each foraging ground in Table 1.

An index of relative abundance or population size was estimated for each site. A standardized method of capture (i.e. tangle net) was used at the Indian River Lagoon and Sebastian Inlet Reef sites, and turtle abundance was estimated as catch per unit effort (CPUE), specifically the number of turtles captured in 1 h with 1 km of tangle net in the water (turtles/km-h) (Ehrhart & Redfoot 1992). Abundance was reported as the mean number of captures per year for the St. Lucie Power Plant Reef site. The Lincoln-Peterson method (Peterson 1896, Lincoln 1930) was used to estimate population size (N) for the Trident Submarine Basin site. This value was obtained by multiplying the total number of turtles captured and marked with paint for identification during 2 consecutive days (n_1) by the total number of marked and unmarked turtles observed during a visual survey conducted on the third day (n_2) and then

Table 1. *Chelonia mydas*. Demographic summary of 497 green turtles (751 growth records) from 4 foraging ground populations in 3 ecologically distinct habitats along the east central coast of Florida. Growth records are given as the total number of growth records in each sample, with the number of growth records resulting from individuals captured on 3 or more occasions in parentheses. Turtle abundance was estimated using 3 different methods: population estimation, CPUE (turtles/km-h), and mean number of captures per year

Foraging ground	Turtles (n)	Growth records (n)	Sampling period	Turtle abundance	Method
Trident Submarine Basin	124	262 (138)	1993–2005	61 ± 10	Population estimation
Indian River Lagoon	132	146 (14)	1982–2005	5	CPUE
Sebastian Inlet Reef	56	58 (2)	1989–2005	12	CPUE
St. Lucie Power Plant Reef	185	285 (100)	1991–2003	281	Mean no. captures

dividing this number by the number of marked animals observed on the third day (m): $N = (n_1 n_2) / m$.

Statistical modeling approach. Juvenile green turtle growth rates were modeled for each foraging ground using a robust nonparametric regression modeling approach (Bjorndal et al. 2000, Seminoff et al. 2002, Balazs & Chaloupka 2004, Chaloupka et al. 2004). The model was fitted to the growth rate data to derive an expected size-specific growth rate function conditioned on informative growth predictors or covariates. A mixed-longitudinal sampling design (sampling with partial replacement) was used with 28% (140/497) of the turtles contributing more than one growth rate value.

The growth rate predictors (covariates) used in the present study were calendar year, mean carapace length (cm SCL), and recapture interval (yr). The year covariate reflects the mean calendar year of the growth rate estimate and was included to account for the implicit time-dependent sampling design inherent in all CMR studies. This covariate accounts for the variability in growth rates that can be attributed to environmental factors or age (cohort) effects. However, as is the case with most wild sea turtle studies, the age of individuals was unknown. Therefore, the effect from environmental factors cannot be distinguished from age (cohort) effects (Chaloupka & Musick 1997). It should also be noted that the year effect is imprecise because most growth records were not based on a 1 yr duration. Recall that the median recapture interval ranged from 1.3 to 1.9 yr, depending on the foraging ground. Nevertheless, the year covariate as defined here is a useful proxy of the year effect and should be included, as it is a sampling design constraint inherent in CMR studies (Chaloupka & Musick 1997). The mean size covariate is the arithmetic mean of the SCL at first or previous capture and subsequent recapture, and is the appropriate metric for describing size-specific growth (Chaloupka et al. 2004). Including recapture interval as a covariate in the model accounts for the potential bias based on variable sampling intervals.

The functional relationships between absolute growth rates and the 3 growth rate predictors were modeled

using a generalized additive mixed modeling approach (GAMM; Chaloupka & Balazs 2005) for the 3 sites in which individual turtles contributed multiple growth rate values (Trident Submarine Basin, Indian River Lagoon, St. Lucie Power Plant Reef). A generalized additive modeling (GAM) approach was used for Sebastian Inlet Reef, where each turtle only contributed one growth rate value. These approaches enable robust analysis of regression models with parametric or fixed effects (site), nonparametric or nonlinear covariates (SCL, year, interval), and non-normal error terms. Turtle-specific random effects were included to account explicitly for individual heterogeneity and potential correlation inherent in mixed-longitudinal data sets (Chaloupka & Balazs 2005). The regression models used here comprised: (1) an identity link, (2) a robust quasi-likelihood error function to minimize outlier effects on parameter estimates, and (3) flexible cubic smoothing splines to model any nonlinear functional form between growth rates and the continuous covariates (year, mean size, recapture interval).

The models were fit to the data using the mgcv package in R (Ihaka & Gentleman 1996, Wood 2006). The nonparametric covariates (year, mean size, recapture interval) were nested within each factor (site). The GAMM and GAM fit summaries used here comprise 2 parts arranged in tabular format for ease of reporting and interpretation (Wood 2006).

RESULTS

Juvenile green turtles captured during the present study ranged in size from 22.8 to 78.6 cm SCL. The size-class distributions of turtles captured at the Indian River Lagoon site and both reef sites were nearly identical, with the majority of turtles measuring between 30 and 50 cm SCL and few turtles greater than 70 cm SCL (Fig. 2). In contrast, the majority of turtles at the Trident Submarine Basin site were smaller than 30 cm SCL and no individuals were larger than 50 cm SCL (Fig. 2). Recapture rates varied by site with the Trident Submarine Basin site exhibiting the highest rate (61%)

and the Sebastian Inlet Reef site exhibiting the lowest (9%). Movement of turtles between sites, documented by recaptures, was minimal ($n = 19$). Growth measurements for turtles initially captured at one site and recaptured at another were not included in the models.

Trident Submarine Basin

From 1993 to 2005, 453 juvenile green turtles were captured 1153 times at the Trident Submarine Basin. More than half of the turtles captured (57%, $n = 259$) were only captured once, and the remaining 43% ($n = 194$) were captured between 2 and 21 times, totaling 700 recapture events or a recapture rate of 61%. Of the 194 recaptured turtles, 124 had capture intervals greater than 10 mo, yielding 262 growth records. Turtles ranged in size from 22.8 to 48.1 cm SCL (mean \pm SD = 29.8 ± 3.8 cm) at initial capture and growth rates were calculated for turtles between 22.9 and 42.7 cm SCL. Recapture intervals ranged from 10.0 mo to 7.6 yr. The estimated population size ranged between 35 and 121 (mean = 61 ± 10 turtles) turtles. Growth rates ranged from -0.2 cm yr⁻¹ (at large for 1.6 yr with absolute growth of -0.3 cm) to 6.9 cm yr⁻¹ (at large for 1.4 yr with absolute growth of 9.8 cm).

Indian River Lagoon

From 1982 to 2005, 2143 green turtles were captured 2442 times at the Indian River Lagoon site. Six turtles were excluded because they were not measured at first capture or they were adults, leaving 2137 immature turtles for the analysis. The majority of turtles (88.1%, $n = 1884$) were captured only once, and 11.8% ($n = 253$) were captured between 2 and 4 times, for a total

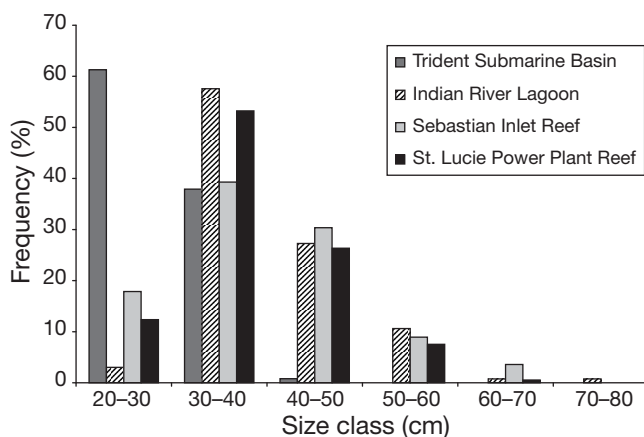


Fig. 2. *Chelonia mydas*. Size class distribution of juvenile green turtles from 4 sites along the east central coast of Florida

of 299 recapture events. Of the 253 recaptured turtles, only 132 were recaptured at intervals greater than 10 mo, yielding 146 growth records. Immature turtles ranged in size from 24.3 to 78.6 cm SCL (mean = 43.7 ± 10.1 cm, $n = 2137$) at initial capture. Growth rates were calculated for turtles ranging in size from 28.5 to 72.3 cm SCL. Recapture intervals ranged from 10.8 mo to 7.3 yr. The mean annual CPUE increased from 1982 to 2005 and varied by time of year (Ehrhart et al. 2007): CPUE was greatest (mean = 7.0 ± 11.1 turtles/km-h) from late autumn through early spring (November–April) and lower (mean = 1.4 ± 2.0 turtles/km-h) from late spring through early autumn (May–October). The mean CPUE from 1982 to 2005 was 2.8 ± 6.3 turtles/km-h. Growth rates ranged from 0.3 cm yr⁻¹ (at large for 4.6 yr with absolute growth of 1.6 cm) to 7.3 cm yr⁻¹ (at large for 1.7 yr with absolute growth of 12.6 cm).

Sabellariid worm rock reef

Sebastian Inlet Reef

From 1989 to 2005, 920 green turtles were captured 1003 times at the Sebastian Inlet Reef site. One turtle was excluded from the analysis because it was an adult, the remaining 919 were immature. The majority of turtles (91.2%, $n = 838$) were captured only once, and 8.8% ($n = 81$) were recaptured. One of the recaptured turtles was 'head-started' by the Florida Department of Natural Resources and was released only 1 yr prior to its first capture at this site. The growth data for this turtle was excluded from the analysis because of the potential effects of the head-starting process on growth. Of the 80 recaptured turtles included in the present study, 56 had capture intervals greater than 10 mo, yielding 58 growth records. Immature turtles ranged in size from 24.7 to 72.3 cm SCL (mean = 41.9 ± 9.9 cm) at initial capture. Growth rates were calculated for turtles ranging in size from 26.0 to 61.9 cm SCL. Recapture intervals ranged from 10.8 mo to 6.0 yr. The mean CPUE from 1989 to 2005 was 18.8 ± 28.9 turtles/km-h. Growth rates ranged from 0.1 cm yr⁻¹ (at large for 11.4 mo with absolute growth of 0.1 cm) to 4.1 cm yr⁻¹ (at large for 1.0 yr with absolute growth of 4.1 cm).

St. Lucie Power Plant Reef

From 1991 to 2003, 2511 green turtles were captured 3668 times at the St. Lucie Power Plant Reef site. Sixty-six adult turtles were excluded, leaving 2445 immature turtles for the analysis. The majority of turtles (81.7%, $n = 1997$) were captured only once, and 18.3% ($n = 448$) were recaptured between 2 and 23 times. Of the

448 recaptured turtles, 185 were recaptured at intervals greater than 10 mo, yielding 285 growth records. Initial capture green turtles ranged in size from 18.7 to 79.0 cm SCL (mean = 39.0 ± 11.0 cm). Growth rates were calculated for turtles ranging in size from 25.0 to 60.5 cm. Recapture intervals ranged from 10 mo to 4.7 yr. The mean number of green turtles captured per year was 281 ± 182.5. Growth rates ranged from -0.18 cm yr⁻¹ (at large for 14.2 mo with absolute growth of -0.2 cm) to 5.7 cm yr⁻¹ (at large for 12.8 mo with absolute growth of 6.1 cm).

GAMM/GAM

The fit of the models for the 4 foraging aggregations given the size-based growth metric is summarized in Table 2. The models comprised one response variable (growth rates in SCL) and 3 growth predictors (mean carapace length, mean year, and recapture interval) nested within each site.

The fit of the GAMMs, represented by nonparametric R² values ranging from 0.08 to 0.28, indicates that there was significant variability in the growth data for these sites. The fit of the GAM for the Sebastian Inlet Reef site was adequate with an R² of 0.503 (deviance explained = 59.6%). Other factors such as individual variability and sex may also be important but were not accounted for in these models.

Overall, the models suggest that growth rates were size-specific for all sites and year-dependent for all except the Indian River Lagoon site. Recapture interval was a significant covariate affecting growth variability for the St. Lucie Power Plant Reef site, but was not significant for the Indian River Lagoon, Sebastian Inlet Reef, or Trident Submarine Basin sites.

Spatial variability in size-specific growth

We found significant differences in growth rates among the sites (Kruskal-Wallis test, $H = 172.01$, $p < 0.01$). Juvenile green turtles from the Indian River Lagoon grew significantly faster than turtles from the other 3 sites (Dunn's multiple comparison test, $p < 0.01$); however, there were no significant differences in growth rates between the 2 reef sites and the Trident Submarine

Basin site ($p > 0.05$). The expected size-specific growth rate functions for the 4 sites are shown together to illustrate the differences among sites (i.e. habitats) and sizes of turtles (Fig. 3). The size at which immature growth rates peak varies among habitats.

Size-specific growth

The models indicate that mean carapace length (cm SCL) had a significant effect on expected growth rates (cm SCL yr⁻¹) for all 4 foraging aggregations (Table 2). Additionally, the mean size growth rate predictor was significantly nonlinear for all 4 aggregations, reflecting a distinct increase in immature growth rates (Fig. 4a,d,g,j). Overall, the size-specific growth rate functions for these foraging aggregations were non-monotonic functions, with growth rates increasing from post-oceanic recruitment size (25 cm SCL) to a maximum which varied by site, before declining to a slower rate when turtles grew to the upper immature size limit for each site (50 cm Trident Submarine Basin; ~70 cm Indian River Lagoon, Sebastian Inlet Reef, and St. Lucie Power Plant Reef). For turtles in the Trident Submarine Basin, growth rates increased to a maximum at about 35 cm SCL and gradually declined thereafter. For turtles at the Indian River Lagoon and

Table 2. Summary of parameter estimates for generalized additive (mixed) models (GAM*/GAMM) fitted to juvenile green turtle growth rates for 4 foraging ground populations along the east central coast of Florida. A significant *F*-value means the covariate was non-linear. Edf: Estimated degrees of freedom; SCL: straight carapace length; ns: not significant; GCV: generalized cross-validation

	Approximate significance of smooth terms			
	Edf	Est. rank	<i>F</i>	<i>p</i>
Trident Submarine Basin				
Mean size (SCL)	2.961	6	4.065	<0.05
Year	4.254	9	10.011	<0.05
Interval	1.535	4	1.308	ns
R ² _{adj} = 0.277, Scale est. = 0.95517, n = 262				
Indian River Lagoon				
Mean size (SCL)	2.419	5	2.861	<0.05
Year	1.654	2	1.738	ns
Interval	1	1	0.133	ns
R ² _{adj} = 0.0779, Scale est. = 1.4462, n = 146				
Sebastian Inlet Reef*				
Mean size (SCL)	3.616	8	3.304	<0.05
Year	6.104	9	3.14	<0.05
Interval	1	1	0.562	ns
R ² _{adj} = 0.503, Deviance explained = 59.6%, GCV score = 0.45251, Scale est. = 0.36107, n = 58				
St. Lucie Power Plant Reef				
Mean size (SCL)	1.497	3	14.097	<0.05
Year	3.61	8	2.843	<0.05
Interval	1	1	16.216	0.05
R ² _{adj} = 0.177, Scale est. = 0.83801, n = 285				

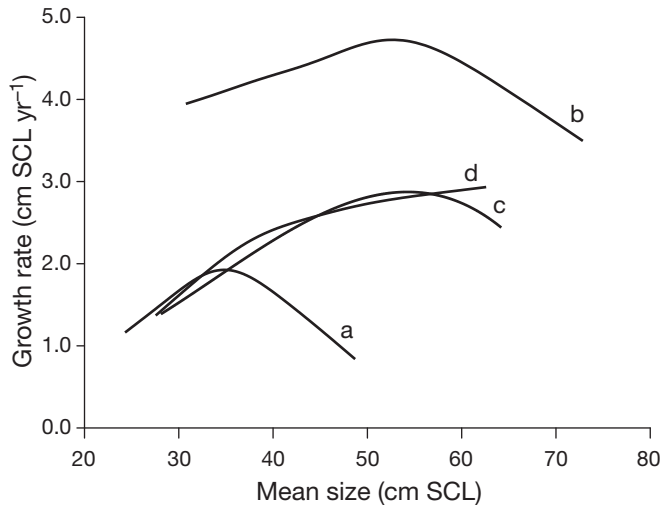


Fig. 3. *Chelonia mydas*. Comparison of size-specific growth rate functions for green turtles from 4 sites in 3 ecologically distinct habitats along the east central coast of Florida: (a) Trident Submarine Basin, (b) Indian River Lagoon, (c) Sebastian Inlet Reef, and (d) St. Lucie Power Plant Reef. SCL: straight carapace length

Sebastian Inlet Reef sites, the peak in growth rates occurred at about 50 to 55 cm SCL. This pattern was not as clearly defined for turtles from the St. Lucie Power Plant Reef site where growth rates continued to increase with carapace length. Although there was no peak in growth rates for turtles at this site, the rate of increase slowed as carapace length increased.

Temporal variability in growth

The models indicate that mean recapture year had a significant effect on expected growth rates (cm SCL yr⁻¹) (Table 2) and was significantly nonlinear for turtles in the Trident Submarine Basin, Sebastian Inlet Reef, and St. Lucie Power Plant Reef sites (Table 3, Fig. 4b,e,h,k). The significant year effect indicates interannual growth variability resulting from

environmental influences on immature growth. Declines in growth rates were evident beginning in 1998 for all sites except the Indian River Lagoon. Growth rates at the Trident Submarine Basin declined steeply through 2000 and continued to decline at a slower rate through 2005. Recapture interval was significant for the St. Lucie Power Plant Reef site only (Table 2, Fig. 4c,f,i,l).

DISCUSSION

The primary findings from this long-term study of green turtle growth dynamics from the east central coast of Florida were: (1) spatial variability in immature growth rates from the same general geographic region, possibly as a result of differences in site ecology; (2) declines in growth rates beginning in 1998 at 3 of the 4 sites; and (3) non-monotonic size-specific growth rate functions reflecting an increase in immature growth rates followed by a gradual decline.

The present study is the first comparative study of growth rates among juvenile green turtles in the Atlantic Ocean. Variability in growth rates of juvenile green turtles has been observed worldwide and comparisons of growth rates between ocean basins have shown that Pacific green turtles grow slower than their Atlantic counterparts (Bjørndal et al. 2000). A comparative study of growth rates of immature green turtles at several sites in the Hawaiian Archipelago showed that turtles in different locations within the Archipelago grow at different rates (Balazs & Chaloupka 2004). Differences in growth rates between populations and among individual turtles can be attributed to a variety of intrinsic (sex, genotype, carapace length) and external factors (habitat, food, year, water temperature, turtle density).

Some early studies on growth were hindered by small sample sizes and short recapture intervals (Mendonça 1981, Shaver 1994), which often led to inflated growth rates and premature estimations of age at maturity. The reliable determination of growth rates of

Table 3. *Chelonia mydas*. Mean (\pm SD) growth rates (cm yr⁻¹) of juvenile green turtles from 4 foraging ground populations along the east central coast of Florida grouped by 10 cm size classes

Size class (cm)	Trident Submarine Basin		Indian River Lagoon		Sebastian Inlet Reef		St. Lucie Power Plant Reef	
	Mean	n	Mean	n	Mean	n	Mean	n
20–30	1.76 \pm 1.46	50	–	–	1.31 \pm 0.72	4	1.18 \pm 0.94	16
30–40	2.30 \pm 1.16	168	3.61 \pm 1.20	51	1.95 \pm 0.84	23	2.14 \pm 1.09	119
40–50	1.57 \pm 1.10	44	4.04 \pm 1.48	57	2.40 \pm 0.77	18	2.51 \pm 1.04	112
50–60	–	–	4.55 \pm 1.12	32	3.00 \pm 0.36	10	2.64 \pm 0.78	35
60–70	–	–	4.04 \pm 1.02	4	2.53 \pm 0.75	3	2.81 \pm 0.89	3
70–80	–	–	2.78 \pm 2.25	2	–	–	–	–

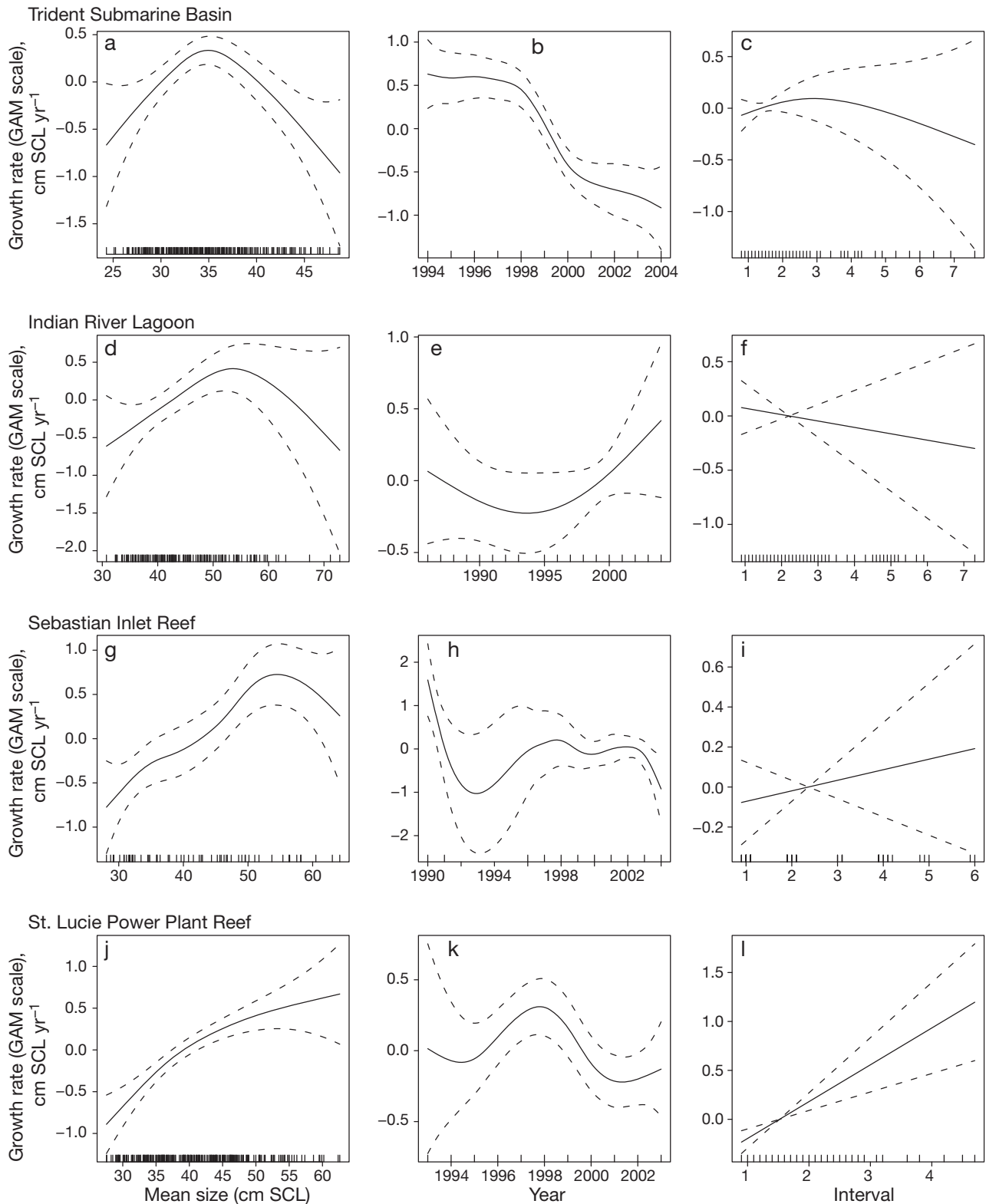


Fig. 4. Graphical summary of generalized additive (mixed) model (GAM/GAMM) fit for each foraging ground summarized in Table 2. (a–c) Trident Submarine Basin; (d–f) Indian River Lagoon, (g–i) Sebastian Inlet Reef, and (j–l) St. Lucie Power Plant Reef. The response variable (growth rate) is shown on the y-axis in each panel as a centered smoothed function scale to ensure valid pointwise 95% confidence bands. Covariates are shown on the x-axis: (a,d,g,j) mean size (between first and next capture, cm SCL); (b,e,h,k) year (growth year index); and (c,f,i,l) recapture interval in years. Solid curves are cubic smoothing spline fits for each continuous covariate conditioned on all other covariates in the GAM/GAMM model for each foraging ground (Table 2), while dashed curves are pointwise 95% confidence curves around the fits

a long-lived species requires large data sets collected over a long time period. Recent studies on growth rates of green turtles utilized large data sets from projects spanning several decades (Bjorndal et al. 2000, Chaloupka et al. 2004). The present study used long-term data and relatively large sample sizes from each site to model growth rates of juvenile green turtles.

Spatial variability in growth rates

The primary factor affecting growth rates of immature green turtles in the present study was habitat type. The Indian River Lagoon, sabellariid worm rock reef, and Trident Submarine Basin are ecologically distinct year-round foraging grounds for immature green turtles. The sabellariid worm rock reef was the only habitat with 2 study sites, and the growth rates at these sites were similar to each other but different from those in other habitats (Fig. 3). Site ecology and health and disease status are 2 potential factors that may contribute to spatial variability in growth rates.

Site ecology

The 3 foraging habitats along the east central coast of Florida primarily differ with respect to algal diversity, algal abundance, and oceanographic conditions. Although red algae are the main dietary component for juvenile green turtles in all 3 habitats, there is variability in the availability and the species of algae they consume. Seven species of red algae made up 82.4% of the vegetation consumed by Trident Submarine Basin turtles, 10 species of red algae made up 83.3% of the vegetation consumed by Indian River Lagoon green turtles, and 22 species of red algae made up 81.2% of the vegetation consumed by reef turtles (Red-foot 1997, Holloway-Adkins 2001). The nutritional quality of the algal species has yet to be determined and may further explain differences in growth rates between sites.

The Trident Submarine Basin is an unusual developmental habitat for green turtles because it is man-made. Available algal forage is limited to the submerged surfaces of the boulders lining the basin and the floating docks. Turtles keep the algal mat cropped short, but they have also been observed foraging on other food items like jellyfish, fish carcasses, bait on hooks, and floating vegetation. The limited amount of algae in the basin is undoubtedly one of the factors limiting the growth of these turtles.

The Indian River Lagoon site is sheltered from ocean waves and the movement of water is primarily driven by wind and tidal current near inlets. The primary food

for green turtles at this site is drift algae (*Bryothamnion seaforthii* and *Gracilariia* spp.) (Holloway-Adkins 2001). The biomass of drift algae in the Indian River Lagoon is considered to be high compared to other areas, but its abundance varies temporally (seasonally and yearly) and spatially (Virnstein and Carbonara 1985, Riegl et al. 2005). Turtles may be temporarily trapped in the lagoon due to the scarcity of exits from this highly productive algae-dominated ecosystem. Free from the stresses of feeding in the rough conditions of the open ocean, turtles can utilize more energy for growth. The accelerated growth rates of turtles from this site as compared to the other sites in the present study are likely related to the high biomass of drift algae and benign foraging conditions.

In contrast, the sabellariid worm rock reefs are located adjacent to the beach in a high-energy wave break zone. With the exception of the calmer summer months (June–August), turtles inhabiting these reefs are subjected to the surge of waves and pounding surf while they forage. The amount of energy required to feed in this type of habitat, as well as to avoid predators like tiger sharks, likely exceeds that of Indian River Lagoon and Trident Submarine Basin turtles and may contribute to the slower growth rates documented at this site. Furthermore, while more than 100 species of algae grow on these reefs (Juett et al. 1976), only a few species (*Laurencia poiteau*, *Hypnea* spp.) were consumed in large quantities by juvenile green turtles (Holloway-Adkins 2001, Gilbert 2005). The abundance and quality of preferred food items may also be limiting the growth rates of these turtles, but without a long-term study documenting changes in the biomass and species composition of algae on the sabellariid worm rock reefs, this hypothesis is speculative.

Health and disease — fibropapillomatosis

Fibropapillomatosis (FP) is a debilitating tumor disease that affects green turtles more than any other species of sea turtle worldwide. The disease was first documented in Florida green turtles in 1937 (Smith & Coates 1938). Turtles that are severely afflicted with the disease are chronically anemic, have heavy parasite loads, and are immuno-suppressed (Work 2005). Growth rates of green turtles in Hawaii were significantly lower for turtles severely afflicted with FP as compared to turtles without the disease (Chaloupka & Balazs 2005). The present study included growth rates of turtles that were mildly and moderately afflicted with FP. Since turtles that are severely afflicted with FP were rarely recaptured, presumably due to reduced survivorship, we could not test for differences in growth rates attributed to FP severity. However, the

site with the highest prevalence of the disease (Indian River Lagoon, 53%) was also the site with the fastest growth rates, which suggests that FP does not have a strong influence on growth rate. The prevalence of FP was much lower in sabellariid worm rock reef turtles (15%), and only one turtle from the Trident Submarine Basin had tumors (Hirama & Ehrhart 2007), yet growth rates for these sites were significantly lower than the Indian River Lagoon site. We conclude that the slower growth rates observed at the Trident Submarine Basin and sabellariid worm rock reef sites are not due to FP.

Temporal variability in growth rates

Declines in growth rates were found in all 3 habitats and may be indicative of density-dependent effects on growth. The foraging aggregations along the Florida coast are comprised of individuals from many nesting stocks, with the greatest contributions coming from those in Costa Rica, Florida and Mexico (Bass & Witzell 2000). Long-term increases in green turtle nest production have been documented in Costa Rica and Florida (Troëng & Rankin 2005, Weishampel et al. 2006, Chaloupka et al. 2008, Ehrhart et al. 2007), presumably resulting in more juveniles recruiting to Florida foraging grounds.

The Trident Submarine Basin encompasses a relatively small area, has a relatively large population of resident turtles with respect to the size of the habitat, and has limited food resources. The recapture rate of 64% indicates that the majority of the turtles are long-term residents, yet growth rates at this site are the slowest in the present study and have been significantly declining since 1998, suggesting a density-dependent effect on growth (Table 2, Figs. 3 & 4b). It is puzzling why the turtles at the Trident Submarine Basin do not leave this habitat in search of better foraging opportunities. The force that drives turtles to move from one developmental habitat to the next is poorly understood, but is likely related to body size and nutrition. One possible explanation for the high degree of site fidelity in a 'crowded' habitat is that even though individuals may not be thriving, they are able to consume enough algae to survive and thus stay in the habitat until their nutritional needs can no longer be met.

The mean CPUE at the Sebastian Inlet Reef site was 18.8 ± 28.8 turtles/km-h and a daily high CPUE of 148 turtles/km-h was recorded in 1999 (Holloway-Adkins et al. 2002). The CPUE data for the Sebastian Inlet Reef site indicate this habitat hosts a very large foraging aggregation of juvenile green turtles. The year effect on growth behavior was significant for both reef sites (Table 2). Density-dependent effects on

growth may be occurring in the reef habitat with declines in growth rates beginning in 1998 at both sites (Fig. 4h,k). Similar declines in growth rates have been documented in the Bahamas and Hawaii (Bjørndal et al. 2000, Balazs & Chaloupka 2004).

The mean CPUE for the Indian River Lagoon site was 2.8 ± 6.5 turtles/km-h. The higher density of turtles at the Sebastian Inlet Reef site compared to the Indian River Lagoon site may be the result of opportunistic settlement. The first neritic habitat newly recruited turtles encounter along the east central coast of Florida is sabellariid worm rock reef, while turtles have to navigate their way in and out of the Indian River Lagoon through one of 5 inlets (e.g. Sebastian Inlet). Capture rates at the Indian River Lagoon site have increased significantly since the inception of the present study, presumably reflecting an increase in the abundance of green turtles at the site (Ehrhart et al. 2007). However, these rates are still substantially lower than capture rates at the Sebastian Inlet Reef site. A temporary decline in growth rates is apparent during the early 1990s (Fig. 4e), but the year covariate made little contribution to the model fit (Table 2). The biomass of drift algae was estimated as ~ 4 tons ha^{-1} near Fort Pierce, Florida, in 1982 (Virnstein & Carbonara 1985) and as ~ 3.8 tons ha^{-1} for the Sebastian Inlet area of the Indian River Lagoon in 2002 (Riegl et al. 2005), but there are no long-term studies on changes in biomass of drift algae in the Indian River Lagoon. A decrease in algal biomass would be expected as turtle density and competition for food increase. More data are needed to confirm density-dependent effects on growth in the Indian River Lagoon.

Non-monotonic size-specific growth rate functions

The dome-shaped or non-monotonic patterns of growth observed for these foraging aggregations are similar to growth rates estimated using skeletochronology for Indian River Lagoon turtles (Zug & Glor 1998), but contradict the results of earlier studies in Florida (Mendonça 1981, Frazer & Ehrhart 1985, Bresette & Gorham 2001). Non-monotonic patterns in green turtle growth rates have previously only been reported from the Pacific Basin — Mexico (Seminoff et al. 2002), Galapagos (Green 1993), Hawaii (Balazs & Chaloupka 2004), and Australia (Chaloupka et al. 2004). The present study is the first time a non-monotonic pattern has been documented in Atlantic green turtles. A population of green turtles in the Bahamas exhibited a monotonic decline in growth with small juveniles (30 cm SCL) growing the fastest at 7 to 8 cm yr^{-1} (Bjørndal et al. 2000). The diet of Bahamian turtles is primarily seagrass, whereas turtles at all sites in the present study foraged primarily on algae.

The reason for the differences in growth patterns between the present study and the Bahamas population is unknown, but may be due to the type and abundance of food items and turtle density.

Accelerated growth in small juveniles (30 to 40 cm) was also observed in an early study of growth in Indian River Lagoon green turtles (Mendonça 1981). This is in contrast to the present study, as well as an earlier skeletochronology study of growth rates of Indian River Lagoon turtles (Zug & Glor 1998), which show faster rates of growth for turtles between 50 and 60 cm and slower rates of growth for smaller and larger turtles. The difference in growth rate between Mendonça's (1981) results and the more recent studies may be attributed to sample size, as the older study used a much smaller data set.

The peak in growth rates at the Trident Submarine Basin was more defined than at any of the other sites. Although speculative, a description and possible explanation regarding size-specific growth rates at this unique site is warranted. For simplicity, size classes are described in 10 cm increments. The smallest turtles (20 to 30 cm) at the Trident Submarine Basin are newly recruited turtles from the oceanic environment. These animals are easily identified by their small size, epibionts on the carapace, sharp marginal edges, and bright white plastron. As they settle in coastal waters, these young turtles switch from an omnivorous to a primarily herbivorous diet. This process can take several months or longer, and may result in slower growth. Furthermore, small turtles recruiting into the Trident Submarine Basin often arrive emaciated and covered in barnacles, an indication of poor overall health and body condition. The combination of a shift in habitat and diet with poor pre-existing body condition could contribute to the slower growth rates of small turtles at this site.

Resident turtles greater than 30 cm in the Trident Submarine Basin have already made the switch to herbivory. These turtles forage on the available algal resources (Redfoot 1997) and are apparently able to consume sufficient amounts of algae to sustain growth at faster rates than both smaller and larger turtles at this site. The slower rates of growth observed in the largest turtles resident in the basin (40 to 50 cm) may be attributed to decreased foraging efficiency due to body and head size. Larger turtles may be unable to forage on food items in cracks and crevices in the boulders available to smaller turtles, restricting them to foraging on the exposed, cropped algal mats lining the basin. The absence of turtles larger than 50 cm indicates that resident turtles approaching this size emigrate from this habitat to other developmental habitats. The quality and quantity of food resources at the Trident Submarine Basin may simply be insufficient to sustain the growth of large turtles.

Growth rates and population recovery

Marine turtle population sizes are typically measured by the number of nests or nesting females (Chaloupka et al. 2008). Therefore, the recovery or growth potential of a population is directly related to time to maturity. Turtles that mature at a younger age will contribute sooner to the growth of their nesting stock. As shown in the present study, the developmental habitat(s) in which a juvenile turtle settles affects its growth rate and ultimately its age at maturity.

In Florida, green turtles suffered severe population declines in the late 1800s as a result of overharvesting by commercial fisheries (True 1887, Wilcox 1896). The species was afforded protection under the U.S. Endangered Species Act in 1978. Further protection was provided in 1992 through a ban on gillnets in Florida. The population appears to be recovering as the relative abundance of juveniles in the Indian River Lagoon system increased by more than 600% from 1982 to 2002 (Ehrhart et al. 2007) and nest production has been increasing since the mid-1990s. The increase in relative abundance closely follows the Archie Carr National Wildlife Refuge green turtle nest production trend (Weishampel et al. 2006), albeit with a 2 yr lag (Fig. 5). This lag corresponds with estimates for recruitment of juveniles from oceanic to neritic habitats at 2 to 3 yr after hatching for the Atlantic (Zug & Glor 1998). The rapid growth rates of Indian River Lagoon turtles combined with a healthy relative abundance of turtles and the protective nature of an inshore developmental habitat may play an important role in

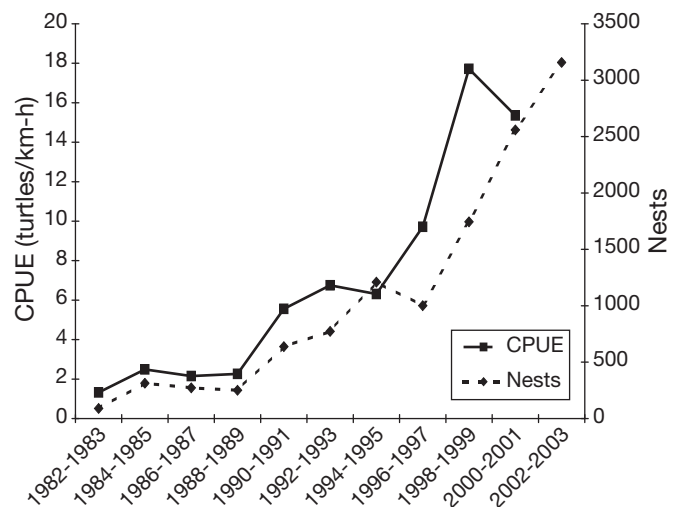


Fig. 5. *Chelonia mydas*. Green turtle nesting trend from the Archie Carr National Wildlife Refuge (dashed line) and winter CPUE of juvenile green turtles from the Indian River Lagoon habitat. CPUE data are time lagged 2 yr to account for time to recruitment. CPUE data reflect year in which new recruits would have hatched from Florida nesting beaches

the rate of growth of the Florida nesting stock and other stocks in the western Atlantic. Further study of foraging aggregations in this region will add to our understanding of immature stages and the population dynamics of the Atlantic green sea turtle.

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