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Author(s) :Tomoharu Eguchi, Jeffrey A. Seminoff, Robin A. LeRoux, Dan Prosperi, Donna L. Dutton, and Peter H. Dutton

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MORPHOLOGY AND GROWTH RATES OF THE GREEN SEA TURTLE (*CHELONIA MYDAS*) IN A NORTHERN-MOST TEMPERATE FORAGING GROUND

Tomoharu Eguchi[1,3], Jeffrey A. Seminoff[1], Robin A. LeRoux[1], Dan Prosperi[1], Donna L. Dutton[2], and Peter H. Dutton[1]

[1]*Protected Resources Division, National Oceanic and Atmospheric Administration Fisheries, Southwest Fisheries Science Center, 3333 N. Torrey Pines Court, La Jolla, CA 92037, USA*
[2]*Ocean Planet Research Inc., 12368 Rue Fountainebleau, San Diego, CA 92131, USA*

ABSTRACT: We examined the morphology and somatic growth rate of Green Sea Turtles living in San Diego Bay, California; one of the northern-most foraging areas for the species in the eastern Pacific. A power plant had discharged heated effluent into the urbanized bay from 1960 to 2010. Straight carapace lengths of 101 Green Sea Turtles were recorded from 31 March 1990 to 15 April 2011 (45.4 to 110.4 cm). Green Sea Turtles in San Diego Bay were morphologically indistinguishable from those foraging in Baja California Sur, Mexico. The median growth rate was 1.03 cm/yr (−1.6 to 11.4 cm/yr) for all turtles and was 4.9 cm/yr for turtles ≤90 cm. These growth rates were one of the fastest for the species in temperate areas and comparable to those reported for tropical regions. The estimated growth parameter of the von Bertalanffy growth function (mean growth coefficient = 0.21, 95% posterior interval = 0.19–0.23) also was greater than for other populations of Green Sea Turtles. Based on behavioral observations and information from other diet studies, we think that the altered environment from the power plant effluent affected the growth of the Green Sea Turtles directly (longer active periods) and via shifts in the environment (changes in prey composition, abundance, and distribution). With the termination of the power plant operation at the end of 2010, the ecosystem is reverting to its natural state, which we expect will result in decreased growth rates of these turtles in the coming years.

Key words: Anthropogenic effects; Endangered species; Growth model; Hierarchical analysis; Power plant; von Bertalanffy

THE GREEN SEA TURTLE (*Chelonia mydas*) inhabits tropical and subtropical neritic environments worldwide (Bowen et al., 1992; Hirth, 1997). Green Sea Turtle populations have declined as a result of human-caused deaths from direct harvest of turtles and eggs and as a result of bycatch in the marine fisheries (National Research Council, 1990; Jackson, 1997; Koch et al., 2006; Humber et al., 2011).

Managing a species requires an understanding of its basic biological characteristics, such as life history traits, spatial and temporal distributions, demography, abundance, behavior, and growth, and how humans affect these characteristics. While many of these parameters have been studied in Green Sea Turtle populations (e.g., Bjorndal et al., 2000; Chaloupka, 2001; Seminoff et al., 2003; Koch et al., 2007), they have been found to vary significantly among populations and possibly among foraging grounds. These differences illustrate that these parameters must be

determined at a smaller scale than at a species level to formulate suitable management strategies for local populations.

Even though Green Sea Turtles have been reported in San Diego Bay, California, USA, since the mid-1800s, the timing and mechanism of their arrival to this temperate foraging ground are unknown (Stinson, 1984; Benson and Dutton, in press). An ongoing and continuous influx of juvenile turtles in the bay indicates that this area is part of the natural range for Green Sea Turtles in the eastern Pacific. Monitoring of these Green Sea Turtles has been conducted since the 1970s (Stinson, 1984; Eguchi et al., 2010). Ongoing genetic studies and satellite telemetry data suggest that this group of turtles is part of the Mexican breeding stocks, most likely originating from nesting beaches in the Revillagigedos and Tres Marias Archipelagos in Mexico (Dutton et al., 2008; Fig. 1).

Green Sea Turtles in San Diego Bay had been associated closely with the effluent of a power plant, which began operation in 1960.

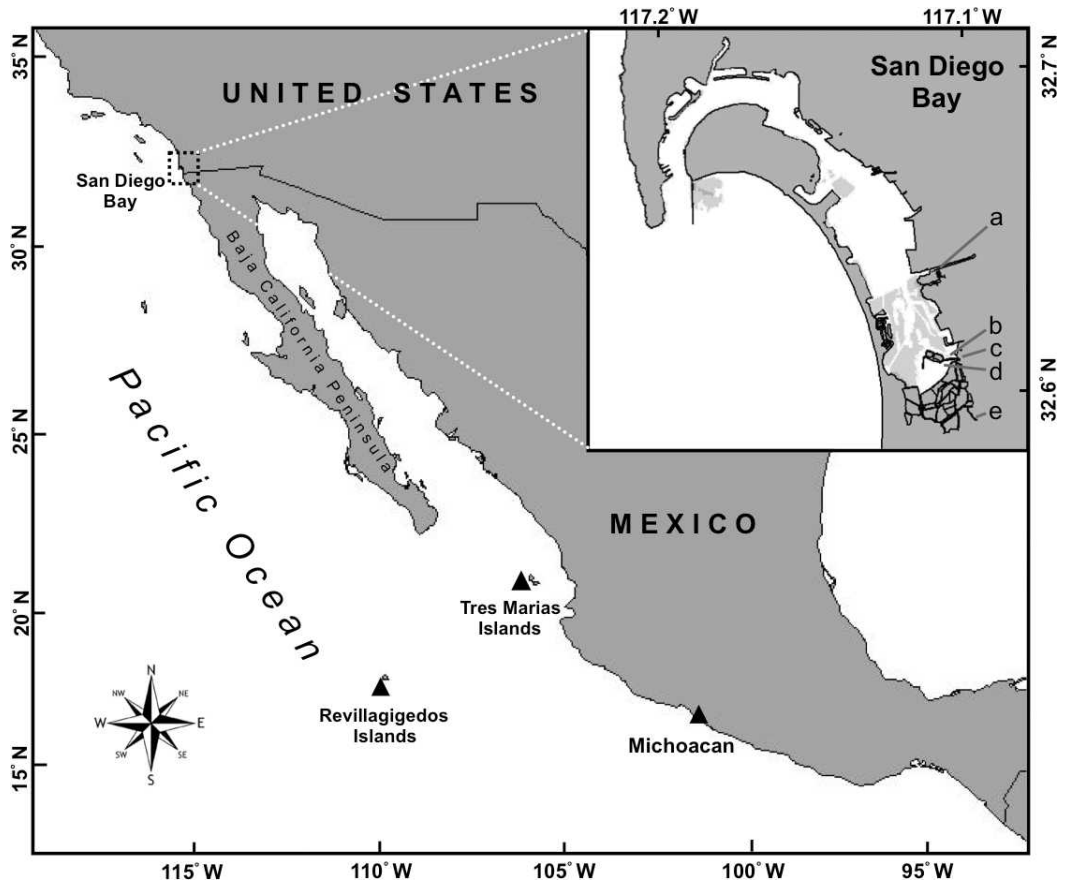[3] CORRESPONDENCE: e-mail, Tomo.Eguchi@noaa.gov

Fig. 1.—Map of the study area in San Diego Bay and known nesting sites for Green Sea Turtles in Mexico. Gray shaded areas within San Diego Bay indicate known eelgrass habitat. (a) Sweetwater River, (b) intake channel, (c) power plant, (d) effluent channel, (e) Otay River. Likely nesting areas are Tres Marias Islands, Revillagigedos Islands, and Michoacán on mainland Mexico.

The power plant discharged warm effluent water used for cooling the plant into the southern end of the bay, which created a unique thermal environment in south San Diego Bay. The consistent pool of warm water (>15°C) created by the power plant effluent attracted the turtles, particularly during the winter when turtles tended to aggregate in the effluent channel as the rest of the bay cooled to temperatures below optimal limits for Green Sea Turtles (<15°C; Felger et al., 1976; Dutton and McDonald, 1990; McDonald et al., 1994; Moon et al., 1997; Seminoff, 2000; Benson and Dutton, in press). This aggregation of Green Sea Turtles has been consistently monitored since the early 1990s, when it became evident that early neritic-stage juvenile turtles first captured and tagged in 1991

were recaptured in the subsequent years in the southern portion of the bay (Dutton and Dutton, 1999; Eguchi et al., 2010). In this study, we use two decades of longitudinal capture records to describe the morphology and somatic growth rate of Green Sea Turtles inhabiting San Diego Bay, California.

The power plant operations ended in December 2010, prompting questions about the possible effects on these turtles in the future. Water temperatures at the study site have reverted to cooler ambient temperatures since closure of the power plant (Fig. 2), and the effects of this on the turtles are unknown (Benson and Dutton, in press; Turner-Tomaszewicz and Seminoff, in press). In this study, our main objective was to describe the somatic
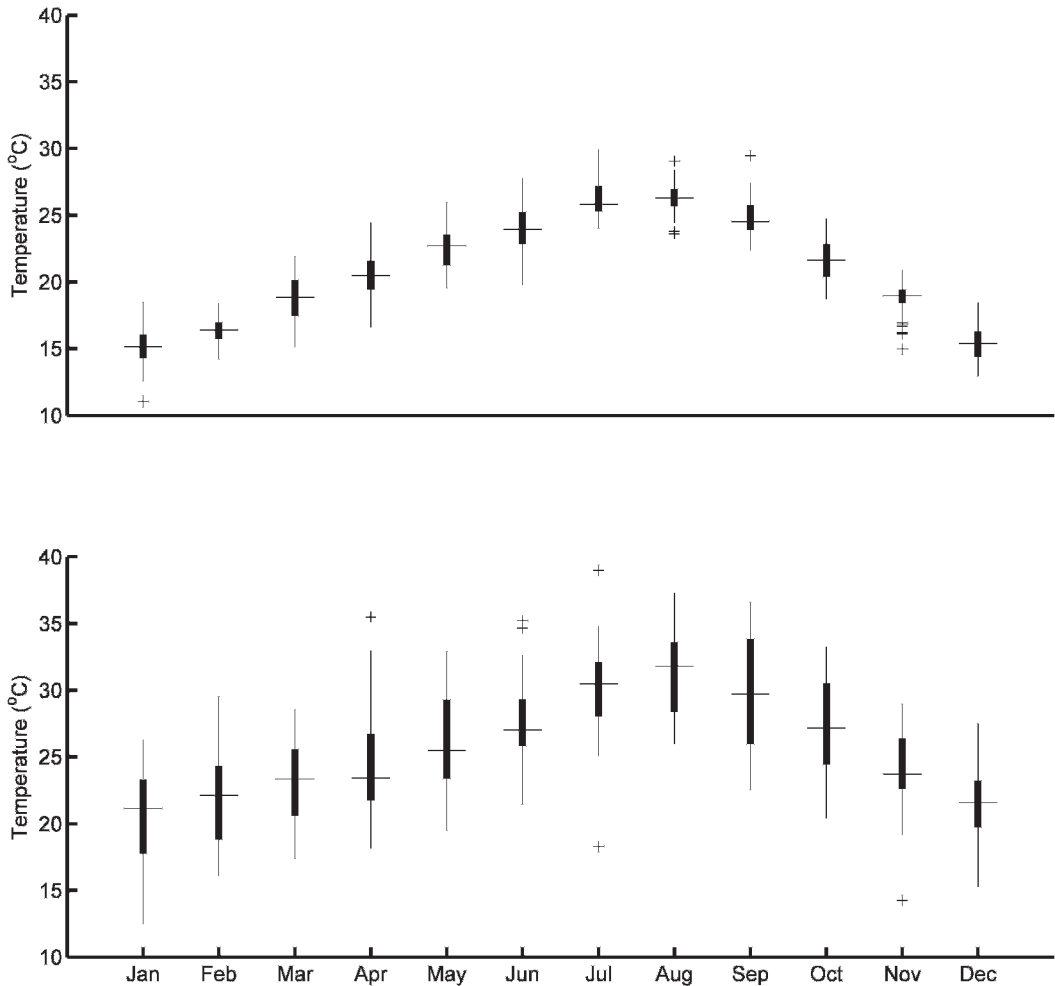
Fig. 2.—Intake (upper panel) and effluent (lower panel) water temperature at the south bay power plant. Data were recorded from 2002 to 2008. Each box indicates 25 and 75 percentiles; horizontal line is the median, and whiskers indicate the approximate 99% range. Data points outside of the 99% range are shown as +.

growth rates of these turtles prior to closure of the power plant in order to evaluate the altered thermal environment on growth rates in the future.

MATERIALS AND METHODS

Details of capturing and handling of Green Sea Turtles in this study can be found in Eguchi et al. (2010). Each capture season started in late autumn (November) to winter (January) and ended in spring (February–May). We measured standard carapace length (SCL) and curved carapace length (CCL) from the nuchal notch to the posterior-most portion of the rear marginal scutes using a Forester's caliper and pliable tape measure, respectively. We used SCL as our length measurement because calipers provide more precise measurements than a tape measure (Bjorndal and Bolten, 1989). Both measurements, however, should provide virtually identical results for the following analyses because there is a strong linear relationship between SCL and CCL (see Results). We recorded mass using a spring scale (prior to 2004) or a digital scale (2004 and later).

Morphological Analyses

We used linear and nonlinear relationships to describe morphological characteristics of Green Sea Turtles. Linear relationships were used to describe relationships between length measurements (curved carapace width [CCL], SCL, and curved carapace width), whereas nonlinear relationships were used to describe length–mass relationship.

All regression analyses were conducted using the Bayesian approach. Normal distributions were used for likelihood functions. Posterior distributions were obtained numerically using Markov chain Monte Carlo (MCMC) using software OpenBugs (v. 3.1.2; Lunn et al., 2009). The mean and 95% posterior interval (PI) were used to provide the point estimate and a measure of uncertainty, respectively. Effects of prior distributions on parameter estimates were determined using two prior distributions (one diffuse and one uni-modal) and comparing results. For each analysis, three chains of 100,000 steps were used while discarding the first 20,000 steps as burn-in samples. The remaining samples were thinned every five steps to reduce autocorrelations among samples. Convergence among chains was examined using the Gelman–Rubin Rhat statistic (Gelman et al., 2004).

Somatic Growth Rates

We first calculated growth rates by linearly interpolating two consecutive measurements that were separated by greater than or equal to 11 mo (Chaloupka and Musick, 1997). These calculations provided a simple measure of linear growth rates. This approach, however, did not account for the effects of repeated measurements of the same individuals, often referred to as "nesting" or, when treated as independent, pseudoreplications (Hurlbert, 1984). To explicitly address and take advantage of repeated measures, we fit a parametric model (the von Bertalanffy growth function) to the data. This parametric approach allowed us to use all data for each individual, regardless of time between two data points. To fit these models, we created two datasets; one with all individuals with at least two measurements (indicated hereafter Data$_{>1}$) and another with individuals with three or more repeated measures (Data$_{>2}$). The comparison of results for these two analyses was

used to determine possible biases from fitting the growth function to two data points.

The von Bertalanffy growth function has the following format:

$$L_t = L_\infty(1 - \exp(-k(t - t_0))), \qquad (1)$$

where L_t is the length at age t, L_∞ is the asymptotic length, k is the intrinsic growth rate, and t_0 is the theoretical age at which the length is zero. Although Fabens (1965) has shown that the model can be converted into an equation of the difference in lengths between two measurements, the growth parameter (k) from the modified approach is not comparable to the same growth parameter for the original format (Francis, 1988). Consequently, we use the original format (Equation 1) in a modified form (Laslett et al., 2002; Eveson et al., 2007; Zhang et al., 2009). The expected length of individual i at the jth capture is modeled as:

$$\hat{L}_{i,j} = L_{\infty,i}\big(1 - \exp\big(-k_i\big(A_i + t_{i,j}\big)\big)\big) \quad (2)$$

where $t_{i,j}$ is the time between captures $j - 1$ and j for individual i and A_i is the age at tagging minus t_0 for individual i (Zhang et al., 2009). The parameter A_i, also referred to as a relative age at tagging (Zhang et al., 2009), is a combination of the theoretical age t_0 and the unknown age at tagging. Consequently, inference cannot be made about either t_0 or the unknown age at tagging alone. It was assumed that the observed length $L_{i,j}$ has the normal distribution with the mean $\hat{L}_{i,j}$ and variance σ^2_L, where the variance increases with the length, while the coefficient of variation (CV), or the ratio between σ_L and the mean, remains constant (Cope and Punt, 2007):

$$L_{i,j} = \hat{L}_{i,j} + \varepsilon_{i,j}$$

where $\varepsilon_{i,j} \sim N(0, \sigma^2_L)$, $\sigma_L = CV \times \hat{L}_{i,j}$, and $\sigma_L > 0$.

We treated these parameters as either population- or individual-specific, i.e., fixed or random effects. For the random-effects model, both parameters were considered to come from parent distributions:

and

$$L_{\infty,i} \sim N\big(\mu_{L\infty}, \sigma^2_{L\infty}\big)$$

$$k_i \sim Beta(\alpha_k, \beta_k),$$

where $i = 1, ..., I$, and I is the total number of individuals in the dataset, $\sigma_{L\infty} > 0$, $\alpha_k > 0$,
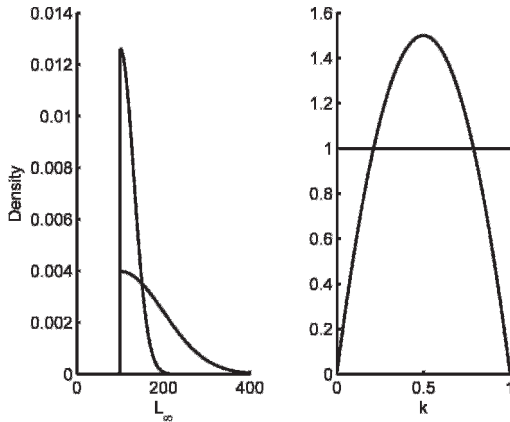
FIG. 3.—Prior distributions for the parameters of the von Bertalanffy growth function fitted for growth data of Green Sea Turtles in San Diego Bay. For L_∞, these are $N(100, \sqrt{(1000)})I(90, \infty)$ and $N(100, \sqrt{(10,000)})I(90, \infty)$, whereas for k, they are Beta(1, 1) and Beta(2,2). Beta(1,1) is the uniform distribution between 0 and 1. $N(a, b)$ indicates the normal or Gaussian distribution with mean a and standard deviation b, $I(a, b)$ indicates the indicator function ($I = 1$ for $a \leq$ and $< b$, and 0 elsewhere). So, $N(a, b)I(c, \infty)$ indicates the normal distribution with mean a and standard deviation b, censored at c. Beta(a, b) indicates the beta distribution with parameters a and b.

and $\beta_k > 0$. For the fixed-effects model, both parameters were considered to be common for all individuals in the population, i.e., $L_{\infty,i} = L_\infty$, and $k_i = k$ for all i. We also considered mixed-effects models, where one parameter was treated as a fixed factor whereas the other parameter was considered as a random factor.

For the prior distributions of L_∞, we constructed a diffuse distribution from the results of the previous studies of morphological characteristics of Green Sea Turtles, where the maximum SCL was >90 cm (Chaloupka et al., 2004; Koch et al., 2007; Goshe et al., 2010; Fig. 3). For the error term, we used Gaussian distributions with large variances, combining process and sampling errors. For hyperparameters for random effects parameters, diffuse prior distributions were used. To assess the effects of prior distributions on posterior distributions, we also analyzed the same dataset with less-diffuse prior distributions on fixed parameters (Fig. 3). Computations were accomplished using OpenBugs. For each model, six independent chains of 150,000 steps were used to sample from posterior distributions, where the first 50,000 steps were discarded as the burn-in samples. To reduce sample auto-correlations, each chain was thinned by taking every 10th sample. Inference on parameters, therefore, was made using 60,000 samples, where the mean and median were used as point estimates and 95% PI as a measure of uncertainty. The difference in MCMC parameters (such as chain lengths, thinning intervals, etc.) from the regression analysis was somewhat arbitrary but based on the complexity of the growth model, which required longer chains, longer burn-in periods, and greater number of chains.

The most appropriate model for our data was determined via deviance information criterion (DIC), combined with the effective number of parameters (pD; Spieglhalter et al., 2002), and posterior simulations. In posterior simulations, growth data were simulated using the growth model and random samples of parameters from the joint posterior distribution. The simulated growth data then were compared to the observed data by evaluating the probability of observed data in the simulated data (Gelman et al., 2004). If the model was reasonable, the simulated data should resemble the observed data. First, the probability of an observed datum (j) in the simulated data was determined (P_j). Second, we determined the proportion of the probabilities (P_j) greater than 0.025 and less than 0.975 for all data (that is, the number of $P_j > 0.025$ and $P_j < 0.975$ for all j divided by n) was computed for each model (P_{95}). The model with the greatest P_{95} was considered the best using this method.

RESULTS

San Diego Bay ranges from approximately 32°43.5'N to 32°36.5'N (datum = WGS84) and is the largest embayment in the Southern California Bight. Open water covers 4262 ha and tidelands cover 1788 ha of San Diego Bay. The bay is approximately 25 km in the north–south direction and has 87 km of shoreline (Lambert and Lambert, 2003; Merkel & Associates, 2009; Fig. 1). Depths range from 15.2 to 22.5 m below mean lower low water (MLLW) in the dredged shipping channels in the northern part of the bay, but most of the bay is less than 15 m below MLLW. In the south bay, water depths are on average less
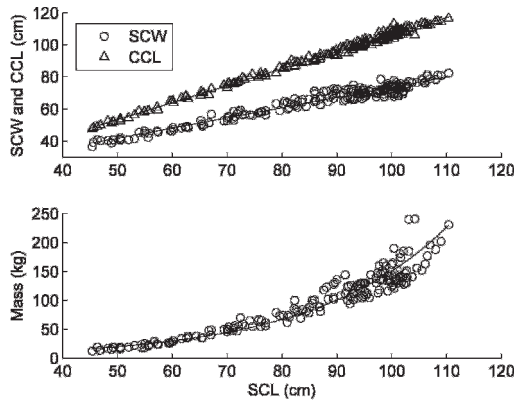
Fɪɢ. 4.—Relationships between standard carapace length (SCL) and standard carapace width (SCW), SCL and curved carapace length (CCL), and SCL and mass. Lines indicate the estimated models for the relationships. Linear models were fit to SCL–SCW and SCL–CCL relationships, whereas an exponential model was fit to the SCL–mass relationship. For estimated parameters and their uncertainties, see Table 1.

than 4.6 m below MLLW (Merkel & Associates, 2009). San Diego Bay contains a variety of habitats, including 333 ha of salt marsh, 396 ha of tidal flats, 431 ha of eelgrass beds, 73 ha of hard substrate and fouling communities, and 3776 ha of mud and sand bottom assemblages (US Navy, Southwest Division, 1999). Freshwater is provided from the Otay and Sweetwater rivers (Fig. 1). The coastline of the bay is populated with private homes, military bases, shipyards, harbors, hotels, restaurants, and industrial docks. A power plant is located on the southeastern shoreline of San Diego Bay. The four units of the power plant began operations in 1960, 1962, 1964, and 1971. Bay water was used to cool the power-generating units and the water was discharged to the bay through the effluent channel. The difference in water temperature between the intake and effluent could be >15°C (Mean = 9.1, SD = 4.84 for 339 records between 1 January 2002 and 30 December 2008; Fig. 2; T. Liebst, personal communication). The power plant was decommissioned at the end of 2010.

Relationships Between Morphological Metrics

From 31 March 1990 to 15 April 2010, a total of 101 individuals were caught 264 times during 115 capture days. Of these 101 turtles, 56 were caught more than once. The distribution of SCL indicated the size of Green Sea Turtles in San Diego Bay spans a wide range (45.4–110.4 cm, median = 92.8 cm; Fig. 4). We observed the largest Green Sea Turtles reported yet in the eastern Pacific (SCL > 110 cm, mass > 200 kg; Fig. 4).

Linear models fit well to the relationships between SCL and CCL (CCL = 0.64 + 1.06 × SCL, $n = 211$, $R^2 = 0.99$; Table 1) and between SCL and standard carapace width (SCW; SCW = 10.11 + 0.63 × SCL, $n = 209$, $R^2 = 0.95$; Table 1). For the relationship between SCL and mass (kg), the exponential model fit the data well (ln(mass) = 0.96 + 0.04 × SCL, $n = 177$, $R^2 = 0.96$; Table 1). Estimated parameters were precise and prior distributions did not affect the results (results not shown).

Somatic Growth Rates

Observed linear growth rates for two measurement pairs separated by at least 11 mo ranged from −1.6 to 11.4 cm/yr, with a median of 1.03 cm/yr (Fig. 5). Twelve measurements from 11 turtles were zero or negative, all of which were for turtles with SCL > 90 cm (Fig. 5; 106 of 183 difference measurements were SCL > 90 cm). For positive growth records, the median was 1.36 cm/yr. Growth rates decreased with increasing size of turtles (Fig. 5). For turtles ≤90 cm the median growth rate was 4.89 cm/yr (Fig. 5).

Posterior simulations and DIC values indicated the random-effects model was the best model (Model 4, Table 2). The effective numbers of parameters (pD) for the random-effects model, however, were negative for the two datasets, indicating DIC may not be an appropriate model selection criterion. The posterior distribution on the mean of the growth coefficient (μ_k) in the model indicated bimodality and a long tail. Differences in P_{95} values between the best and second-best models were less than 1% for the both datasets (Table 2). Consequently, we used Model 3 as our best model. Although not shown, the differences in parameter estimates among the models were trivial. Differences in parameter estimates between the two datasets (Data$_{<1}$ and Data$_{<2}$) also were negligible

TABLE 1.—Summary statistics of regression analyses between standard carapace length (SCL;cm) and other measurements. Linear models were fit to curved carapace length (CCL; cm) and standard carapace width (SCW; cm), whereas an exponential model was fit to mass (kg). The error term (ε) is modeled with a normal distribution with mean 0 and standard deviation σ; $\varepsilon \sim N(0, \sigma)$. Point estimates are means of posterior distributions, whereas uncertainties are expressed in 95% posterior intervals (PI). Vague prior distributions were used for the analysis: β_0 and $\beta_1 \sim N(0, 100)$, and $1/\sigma^2 \sim GAM(0.001, 0.0001)$.

Model	Estimates [95% PI]		
	β_0	β_1	σ
CCL = β_0 + β_1SCL + ε	0.64 [−0.44, 1.70]	1.06 [1.04, 1.07]	1.49 [1.36, 1.65]
SCW = β_0 + β_1SCL + ε	10.11 [8.39, 11.84]	0.63 [0.61, 0.65]	2.39 [2.18, 2.65]
ln(Mass) = β_0 + β_1SCL + ε	0.96 [0.86, 1.07]	0.04 [0.04, 0.04]	0.14 [0.13, 0.16]

(Table 3). The mean of the hyperdistribution of asymptotic length ($\mu_{L\infty}$) of the Green Sea Turtles was estimated to be approximately 102 cm (95% PI = 99.5–104.6), whereas the mean of the standard deviation of the asymptotic length ($\sigma_{L\infty}$) was 5.5 cm (95% PI = 3.87–7.81). For each turtle, the median $L_{\infty,i}$ ranged from 91.3 to 112.0 cm. The intrinsic growth rate parameter (k) was estimated to be 0.2 (95% PI = 0.19–0.23). Qualitatively, the model fit well to the data (Fig. 6).

DISCUSSION

Morphological Analyses

The linear relationship between CCL and SCL for Green Sea Turtles in San Diego Bay was similar to that reported for Green Sea Turtles at a coastal foraging ground in Bahia
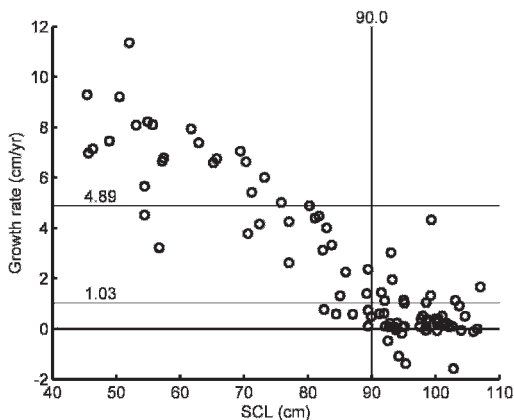

FIG. 5.—Growth rates as measured by differences between two standard carapace length measurements divided by the elapsed time (>11 mo) of Green Sea Turtles caught in San Diego Bay from March 1990 to April 2010. Horizontal lines indicate the median for all turtles (1.03 cm/yr) and for turtles ≤90 cm (4.89 cm/yr).

de los Angeles, Baja California Sur, Mexico (28°58′N, 113°33′W) by Seminoff et al. (2003, who reported that CCL = 2.25 + 1.04 × SCL, R^2 = 0.95). The reported slope for the Mexican foraging ground was within the 95% PI for the San Diego Bay turtles (1.04–1.07), which indicated the similarity in the carapace shape (SCL–CCL relationship) between the two groups. The difference in intercepts (2.25 vs. 0.64) indicated, however, for a given SCL, Green Sea Turtles in Bahia de los Angeles had deeper bodies than turtles in San Diego Bay. The biological difference between these two estimates, however, probably was insignificant (<2 cm). The estimated parameters for the exponential model between SCL and mass were also similar to those reported for the Green Sea Turtles in Baja, Mexico by Seminoff et al. (2003, who reported that ln[mass] = 1.05 + 0.04SCL, R^2 = 0.86). The slope estimates were virtually identical whereas the intercept for the Baja dataset was within the 95% PI (0.86–1.07) for the San Diego dataset. These results indicated that morphologically these turtles at the two foraging grounds are indistinguishable, even though these two foraging groups may be demographically separate. Preliminary results from genetic studies suggest that Green Sea Turtles in Bahia de los Angeles largely come from the Michoacán (mainland) Mexico nesting rookery, whereas those in San Diego Bay come primarily from the Revillagigedos Archipelago rookery (Dutton, 2003; Dutton et al., 2008; P. Dutton, personal observation).

Somatic Growth Rates

The slow median growth rate (1.03 cm/yr) of Green Sea Turtles in San Diego Bay was probably because of the size distribution of

TABLE 2.—Model selection statistics for estimating the parameters of the von Bertalanffy growth function for Green Sea Turtles in San Diego Bay. DIC is the deviance information criteria and pD is the effective number of parameters (Spiegelhalter et al., 2002). The column for P_{95} indicates the fit of each model to data as it is evaluated via posterior simulations (see text for details). The best model for each dataset is in bold for each of two model selection criteria (DIC and P_{95}).

Model	Data	DIC	pD	P_{95}
1: L_∞ = fixed, k = fixed	Data$_{>1}$	982.0	41.9	0.993
2: L_∞ = fixed, k = random	Data$_{>1}$	880.5	20.8	0.996
3: L_∞ = random, k = fixed	Data$_{>1}$	**748.5**	54.3	0.998
4: L_∞ = random, k = random	Data$_{>1}$	312.9	−225.3	**0.999**
1: L_∞ = fixed, k = fixed	Data$_{>2}$	743.8	27.9	0.995
2: L_∞ = fixed, k = random	Data$_{>2}$	677.8	22.6	0.997
3: L_∞ = random, k = fixed	Data$_{>2}$	**575.8**	43.6	0.997
4: L_∞ = random, k = random	Data$_{>2}$	289.1	−116.9	**0.999**

these turtles that were caught multiple times (Fig. 5). Most of the negative growth measurements are likely the results of measurement errors. For smaller turtles (SCL ≤ 90 cm), however, the observed growth rates of 43 measurements from 22 individuals (median = 4.89 cm/yr and up to 11.35 cm/yr) were comparable to those from the southern Bahamas (median = 4.3 cm/yr, and up to 10.8 cm/yr, reported by Bjorndal et al., 2000), Puerto Rico (mean = 5.08 ± 0.83 [SE] cm/yr reported by Collazo et al., 1992), and the central east coast of Florida, USA (up to 7.3 cm/yr reported by Kubis et al., 2009). For these 43 measurements, 28 were greater than 4 cm/yr (Fig. 5). Green Sea Turtles in San Diego Bay exhibited among the fastest growth rates reported for this species in temperate regions (<2.2 cm/yr reported by Limpus and Chaloupka, 1997; <3.4 cm/yr reported by Seminoff et al., 2002; <3.5 cm/yr reported by Chaloupka et al., 2004; <3.0 cm/yr reported by Koch et al., 2007; and <3.1 cm/yr [mean] reported by López-Castro et al., 2010).

The estimated parameters of the von Bertalanffy growth function also indicated the rapid growth of these Green Sea Turtles.

The estimated growth coefficient (median k = 0.20, 95% PI = 0.19–0.23) was greater than that for Green Sea Turtles in Bahía Magdalena, Mexico, approximately 1000 km south of San Diego Bay (k = 0.04 reported by Koch et al., 2007) or in the coastal waters along the southeastern United States (k = 0.02, 95% confidence interval = 0.01–0.03 reported by Goshe et al., 2010). These comparisons showed that the growth coefficient was about 5 to 10 times greater for the San Diego Bay Green Sea Turtles than for the Baja turtles or Atlantic Green Sea Turtles along the southeastern coast of the United States. Combined with the linear growth rate measurements, it was apparent that the juvenile Green Sea Turtles in San Diego Bay grew fast, especially considering the latitude at which they overwinter.

The rapid growth of juvenile Green Sea Turtles in San Diego Bay most likely was attributable to the physical environment. Green Sea Turtles in San Diego Bay have been strongly associated with the warm effluent from the power plant (Eguchi et al., 2010; Turner-Tomaszewicz and Seminoff, in press). We observed Green Sea Turtles in the effluent channel during winter months when

TABLE 3.—Estimated parameters for the von Bertalanffy growth function for Green Sea Turtles in San Diego Bay. Two datasets indicate all turtles with more than one measurement (Data$_{>1}$; n = 52) and more than two measurements (Data$_{>2}$; n = 30). Statistics are means, medians (in italic), and 95% posterior intervals in brackets.

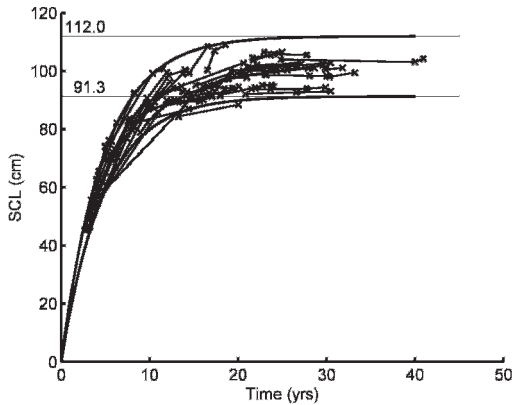| Model	Data	$\mu_{L\infty}$	$\sigma_{L\infty}$	k
L_∞ = random, k = fixed	Data$_{>1}$	101.8	5.33	0.21
		101.8	*5.28*	*0.21*
		[99.9,103.9]	[4.02,6.97]	[0.19,0.23]
	Data$_{>2}$	101.9	5.53	0.21
		101.9	*5.42*	*0.21*
		[99.5,104.6]	[3.87,7.81]	[0.19,0.23]

FIG. 6.—Observed data (connected xs) overlaid with a von Bertalanffy growth function with estimated parameters from the best model (Model 3). The minimum and maximum of $L_{\infty,i}$ (91.3 and 112.0 cm) and the mean of growth parameter ($k = 0.208$) were used. For growth data of the ith turtle, the posterior mean of A_i was added to the observed records, where A_i is the age at tagging minus theoretical age at which the length is zero. The intercepts of the fitted curves were fixed at zero.

the rest of the bay and the coastal water were too cold for the turtles to be active.

The sea surface temperature of the California current along the Southern California Bight and the northern Baja Peninsula is approximately 14°C during winter months (Hickey, 1993; Hood, 1993; Legaard and Thomas, 2006), which is less than the lower limit of thermal range for Green Sea Turtles. The water temperature outside of the effluent also is less than 15°C during winter months. Consequently, it is likely that the water mass along the coast and in the northern bay would act as a thermal barrier for these turtles in winter, discouraging them from moving out of the bay.

As ectotherms, turtles rely on the ambient environmental temperature to support physiological processes such as digestion and growth (Avery et al., 1993). Thornhill (1982) observed a similar trend in a freshwater turtle species, the Red-eared Slider, *Trachemys scripta elegans*, in a lake warmed by effluent from a power plant. The reproductive potential, measured by the mean clutch size times the mean number of clutches per year, of turtles in the lake was greater than that of the same species in a nearby natural lake. The turtles in the effluent lake were growing and

maturing faster, which probably was caused by the longer active periods due to the warm water temperature during winter periods when the turtles in the natural lake were inactive.

Gibbons (1970) also noted that Yellow-bellied Sliders, *Trachemys scripta scripta*, living in a pond that received heated effluent from a nuclear reactor in South Carolina were larger and growing faster than conspecifics living in nearby ponds. Gibbons (1970) concluded that the difference was not directly related to the anthropogenic thermal environment due to the warm effluent but indirectly associated with greater food abundance and variety in the pond compared with the nearby ponds. Higher water temperatures likely increased the productivity and provided turtles with greater diet possibilities; Yellow-bellied Sliders in the pond consumed diets high in protein, whereas the same species in other areas exclusively fed on aquatic plants (Gibbons, 1970).

For Green Sea Turtles, differences in growth rates among foraging habitats have been reported for the Hawaiian Archipelago (Balazs, 1995; Balazs and Chaloupka, 2004), the Great Barrier Reef, Australia (Chaloupka et al., 2004), and the central east coast of Florida (Kubis et al., 2009). These researchers have suggested diet as the main factor affecting these differences. For example, available diet within a foraging ground may be affected by local environment (Chaloupka et al., 2004; Kubis et al., 2009) and digestibility of certain diet may be greater than others (Balazs, 1995; Bjorndal, 1997). The combination of high water temperature and protein-rich food has been reported to increase the growth rate in a freshwater turtle species (Avery et al., 1993). It is likely that such an effect existed for the Green Sea Turtles in San Diego Bay. Dietary analysis of the Green Sea Turtles in San Diego Bay has revealed that invertebrates are a significant source of the diet (24–56%, median = 38%; Lemons et al., 2011). Consequently, the growth rates of Green Sea Turtles in San Diego Bay have probably been influenced directly and indirectly by the altered environment from the power plant effluent. The change in the thermal environment in south San Diego

Bay due to the recent termination of the power plant will likely affect the distribution, composition, and abundance of potential prey items of Green Sea Turtles. As the thermal environment in the bay returns to its ambient natural state, the growth rates of juvenile Green Sea Turtles in the bay may approach those found along the coast of the Baja California Peninsula, Mexico.

Throughout the study, Green Sea Turtles in San Diego Bay were caught during winter months, from October through May. Consequently, within-year variability in growth rates was not considered in this study. The seasonal differences in somatic growths of Green Sea Turtles have been observed at other locales, including the coast of the Baja Peninsula, Mexico (Koch et al., 2007) and at South Padre Island, Texas, USA (Coyne, 1994). In San Diego Bay, however, ambient water temperature in the effluent channel during the winter months was close to that in the intake channel during the summer months (Fig. 2). Consequently, it is plausible that these turtles were in a somewhat constant thermal environment throughout the year because of the power plant effluent.

The use of power plant effluent as a thermal refuge by wildlife is not new. For example, the Florida Manatee (*Trichechus manatus latirostris*) has been observed to take advantage of the warm effluent of power plants in winter (Laist and Reynolds, 2005a). Loss of warm water has been considered as a long-term significant threat to the species in the area (Laist and Reynolds, 2005b; Runge et al., 2007). Unlike the case with Florida manatees, however, we do not expect the change in water temperature to be a significant threat to these Green Sea Turtles in San Diego Bay. The expected responses of Green Sea Turtles to the changing thermal environment in San Diego Bay include (1) inactivity during winter months when water temperature is <15°C; (2) higher concentrations of turtles to the warmest part of the bay (southern extreme) during late autumn, winter, and early spring; and (3) decrease in somatic growth rates. There is concern that the chance of collisions between fast-moving watercrafts and turtles may increase in the south bay while the water temperature is low. To understand how these turtles change their behavior and distribution in response to the change in their thermal environment, we continue to monitor the movements and behavior of the Green Sea Turtles in the bay.

In conclusion, Green Sea Turtles inhabiting San Diego Bay exhibited growth rates among the fastest reported for this species, likely owing to the anthropogenic thermal environment created by a power plant. The potential consequences of these fast growth rates for this foraging population include increased reproductive output from early maturity, as has been reported for freshwater turtles (e.g., Thornhill, 1982). However, it is unclear what will happen now that the waters at our study site have cooled to an ambient state as of January 2011, following closure of the power plant. We have already witnessed changes in the San Diego Bay ecosystem, e.g., reduction in bryozoans and increase in eelgrass at some areas, and increased captures of sluggish turtles in winter. Our results provide a baseline on growth rates prior to the closure of the power plant and continuous monitoring of the turtles and the ecosystem in the bay will provide necessary information about the change in the growth rates and the effects of changing environment on these turtles in the future.

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