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Estimation of survival rates of loggerhead sea turtles (*Caretta caretta*) in Japan using a novel framework

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ABSTRACT

Loggerhead sea turtles are an endangered species, and effective management requires accurate survival estimation. Narrow-interval estimates are particularly necessary in Japan because the available survival estimates have intervals that are too wide to allow comparison with estimates from other regions. Catch-curve analysis is a method for survival estimation and has limitations in that the existing framework cannot consider growth curve errors and sea turtle immigration. However, catch-curve analysis does not suffer from the requirement for intensive research efforts compared with mark-recapture analysis. Therefore, in this study, a new estimation framework was developed that can account for growth curve errors and turtle immigration, and the population parameters of loggerhead turtles (*Caretta caretta*) in Muroto, Japan between July 2002 and November 2009 were estimated. Using the developed framework, the survival rate was estimated as 0.852 year^{-1} (95% highest-density interval: 0.799–0.903). Compared with the Baja California loggerhead population, the results suggest that the survival rate after immigration to Japan is lower than that before immigration. For loggerhead sea turtles, which generally exhibit higher survival rates as they grow, this result suggests the presence of factors such as bycatch that increase mortality around Japan.

1. Introduction

Loggerhead sea turtles are listed as Endangered in the IUCN Red List (IUCN, 2022). In Japan, the total number of nesting loggerhead sea turtles is showing a long-term decreasing trend (Kamezaki et al., 2003; Sea turtle conference in Japan, 2007), and the accurate estimation of their survival rates is necessary for effective management (Caswell, 2000).

Several studies have estimated the survival rates of loggerhead turtle populations in other regions (Bjorndal et al., 2003b; BraunMcNeill et al., 2007; Casale et al., 2007, 2015; Chaloupka and Limpus, 2002; Frazer, 1987; Hatase et al., 2013; Monk et al., 2011; Phillips et al., 2014; Sasso et al., 2006), and comparing these survival rates with that of the Japanese population is essential to determine the mortality factor. In particular, as North Pacific loggerhead turtles migrate to Japan after spending their juvenile period in the Northeast Pacific region, comparing survival rates before and after immigration is important. However, few studies have estimated survival rates in Japan apart from that by Hatase et al. (2013), who estimated the survival rate of adult females on Yakushima Island as 0.871 year^{-1} (95% confidence interval (CI): 0.689–1.053 year^{-1}). As their CI, which is interpreted as an indicator of estimation accuracy, exceeded 1 and violated the assumptions of survival rates, using this value for comparison is difficult. Therefore, estimating survival rates with smaller estimation intervals is essential to make the survival rate comparable with those in other regions.

Two methods are generally used to estimate sea turtle survival rates: mark-recapture and catch-curve analyses. Mark-recapture analysis estimates survival rates from the encounter data of tagged individuals (application to loggerheads: BraunMcNeill et al., 2007; Casale et al., 2007; Chaloupka and Limpus, 2002; Hatase et al., 2013; Monk et al., 2011; Phillips et al., 2014; Sasso et al., 2006). The development of frameworks for mark-recapture analysis has enabled the consideration of transient individuals (Chaloupka and Limpus, 2002; Pradel et al., 1997; Sasso et al., 2006), the use of recognition and stranding data (Barker, 1997; BraunMcNeill et al., 2007; Casale et al., 2007), and the inclusion of state transitions (Hatase et al., 2013; Kendall, 2004; Monk et al., 2011; Phillips et al., 2014). Despite these advantages, this type of analysis requires extensive tagging and time-intensive research efforts (Casale et al., 2015). This limitation often results in low recapture rates and thus results in wide intervals in survival rate estimates (Monk et al., 2011; Phillips et al., 2014; Sasso et al., 2006). Loggerhead turtles in Japan are divided into three management units (Ryukyu,

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Yakushima, and mainland Japan) through mtDNA analysis (Matsuzawa et al., 2016); therefore, a large research area covering each group is desirable to achieve a high recapture rate. However, such large research areas are not realistic and an increase in the estimation intervals is inevitable.

In catch-curve analysis, the growth curve, or the relationship between the age and carapace length, is estimated using the humerus and carapace length (application to loggerheads: Avens et al., 2013, 2015; Bjorndal et al., 2003a; Casale et al., 2011; Guarino et al., 2020; Lenz et al., 2016; Parham and Zug, 1997; Petitet et al., 2012; Piovano et al., 2011; Ramirez et al., 2017; Snover et al., 2010; Tomaszewicz et al., 2015). The growth curve is subsequently used to convert the carapace length distribution into an age distribution, and several estimators are employed to estimate survival rates from the age distribution (application to loggerheads: Bjorndal et al., 2003b; Casale et al., 2015; Frazer, 1987). Four concerns have been identified in terms of catch-curve analysis:

C1: Estimation errors of the growth curve are not considered (Bjorndal et al., 2003b; Frazer, 1987).
C2: The effects of immigration or emigration cannot be distinguished from survival estimates (Bjorndal et al., 2003b).
C3: The survival rate is considered constant, irrespective of the size and age of the sea turtles (Bjorndal et al., 2003b; Casale et al., 2015).
C4: The age distribution is assumed to be stable over the study period (Bjorndal et al., 2003b; Casale et al., 2015; Frazer, 1987).

C1 reduces the reliability of the estimates because the growth of sea turtles varies significantly among individuals; thus, the estimated growth curve contains large variations. C2 causes a large estimation bias because the loggerhead turtles observed in Japan are immigrants (see the Discussion for considerations regarding C3 and C4). Despite these concerns, catch-curve analysis requires less research effort than mark-recapture analysis and is therefore less hindered by limitations on research efforts (Casale et al., 2015). Thus, catch-curve analysis can be a useful estimation method if an appropriate analytical framework is established and the aforementioned concerns are resolved. In this study, C1 is resolved as described in Section 2.2.1 using the prior distribution of a Bayesian estimation framework considering growth curve errors. In addition, C2 is resolved in Section 2.2.2 using a mathematical model that includes immigration.

2. Material and methods

2.1. Material

This study used two available types of data on loggerhead sea turtles: the straight carapace length (SCL) and humerus data.

The SCL data were collected from incidentally captured individuals in Muroto, Kochi Prefecture, Japan (33°15′N, 134°11′E), from July 2002 to November 2009, and comprised 1392 individuals (mode: 74.0–74.9 cm class; range: 56.3–105.0 cm; see Ishihara et al., 2011 for details). However, one of the 1392 individuals was excluded from this analysis because it had a carapace length of 105.0 cm, which is well outside the general size range of loggerhead turtles in the waters around Japan.

The humerus data were collected in Ishihara (2011) from 85 dead loggerhead turtles. Among these, 79 turtles were found in large pound nets or stranded ashore on the Japanese coast, and 6 hatchlings were collected from different nests. As the lines of arrested growth (LAGs) of the humerus mostly remain between the minimum width and deltopectral crest (Zug et al., 1986), the humeri were cut in place using a circular saw and honed to be less than 1 mm thick. Although the number of unabsorbed LAGs differed at each end, the radii and widths of the LAGs were measured along the major axis using a reading microscope (KENIS Ltd., NRM-2XZ/KN3102250) under transmitted light. The bone sections were soaked in glycerin, and 654 sets of humerus radius and the width data of the LAGs were determined without staining.

2.2. Model construction

It is necessary to evaluate the estimation errors of the growth curve (C1) and construct a new estimator that accounts for immigration (C2) to estimate the survival rates of loggerhead turtles using catch-curve analysis accurately.

The frequentist or Bayesian approaches are mainly used for statistical model building, and most estimators in catch-curve analysis are constructed using the former approach. However, compared with the frequentist approach, the Bayesian approach has the advantage of explicitly incorporating prior knowledge into the analysis and allowing for flexible model construction (Gelman et al., 2013; Kruschke, 2014; McCarthy, 2007). In addition, the constructed posterior distribution can be interpreted as the probability that is obtained by the true parameters under the model assumptions, and an intuitive interpretation can be made for intervals (known as the highest-density intervals (HDIs)) (Gelman et al., 2013; Kruschke, 2014; McCarthy, 2007). Therefore, the Bayesian approach is appropriate for solving the analytical problem of catch-curve analysis and comparing the estimation results among populations.

In the Bayesian approach, the likelihood function $f(\boldsymbol{X} \mid \theta)$ and prior distributions $\pi(\theta)$ are set, where X is a variable and θ is a parameter. The likelihood function is constructed from a model, and the prior distributions are set using prior information on the model parameters. Subsequently, the posterior distributions $p(\theta \mid \boldsymbol{X}) \propto f(\boldsymbol{X} \mid \theta) \cdot \pi(\theta)$ of the parameters are calculated using methods such as Markov chain Monte Carlo (MCMC). By specifying the likelihood function and prior distributions, it is possible to incorporate prior information and achieve flexible survival estimation.

Using this Bayesian statistical framework, this study aimed to solve the aforementioned analytical concerns, as follows:

Section 2.2.1: The parameters of the growth curve estimated from the humerus data were used as a prior distribution in the analysis of the carapace length distribution.
Section 2.2.2: A likelihood function was constructed to consider immigration and survival separately and explicitly.

Kindly refer to the manual and scripts in the repository for specific instructions on estimating survival rates using specific data or performing simulations.

2.2.1. Consideration of growth curve errors

Errors in the estimated growth curve were considered by extending the regression protocol of Parham and Zug (1997). The sea turtle humeral radius H is expressed as a Bertalanffy growth equation (Von Bertalanffy, 1938), assuming that the growth rate decreases with growth, as follows:

$$H(t) = H_m(1 - e^{-G_h t}), \tag{1}$$

where $H_m(> 0)$ denotes the maximum humeral radius, $G_h(> 0)$ denotes the growth coefficient of the humerus, and t denotes the age of the sea turtle. Depending on the radius of the sea turtle humerus, the LAG width $\delta H(H)$ can be expressed as follows (Allen, 1966; Parham and Zug, 1997):

$$\delta H(H) = (e^{-G_h} - 1)(H_m - H). \tag{2}$$

Assuming that the LAG width data $\boldsymbol{\delta H} = (\delta H_1, \delta H_2, \ldots, \delta H_i, \ldots, \delta H_I)$ (where I denotes the total number of humerus data points corresponding to radius $\boldsymbol{H}_i = (H_1, H_2, \ldots, H_i, \ldots, H_I)$) follow a normal distribution with a mean of (2) and standard deviation $\sigma(> 0)$, the likelihood function of the model can be expressed as follows:

$$f(\boldsymbol{H}_i, \boldsymbol{\delta H} \mid H_m, G_h, \sigma) \propto \prod_{i=1}^{I} \frac{1}{\sigma} \exp\left(- \frac{\{(e^{-G_h} - 1)(H_m - H_i) - \delta H_i\}^2}{2\sigma^2} \right). \tag{3}$$

We use a half-infinite uniform distribution for the prior distribution of H_m, G_h, and σ, as follows:

$$\pi(H_m)\begin{cases} C_{H_m} & \text{if } \ H_m > \max \boldsymbol{H}_i \\ 0 & \text{else} \end{cases}, \quad \pi(G_h)\begin{cases} C_{G_h} & \text{if } \ G_h > 0 \\ 0 & \text{else} \end{cases}, \quad \pi(\sigma)\begin{cases} C_\sigma & \text{if } \ \sigma > 0 \\ 0 & \text{else} \end{cases}. \tag{4}$$

In this case, the posterior distribution of these parameters can be expressed as

$$\begin{aligned} & p(H_m, G_h, \sigma \mid \boldsymbol{H}_i, \boldsymbol{\delta H}) \\ & \quad \propto p(\boldsymbol{H}_i, \boldsymbol{\delta H} \mid H_m, G_h, \sigma) \cdot \pi(H_m) \cdot \pi(G_h) \cdot \pi(\sigma) \\ & \quad \propto \begin{cases} p(\boldsymbol{H}_i, \boldsymbol{\delta H} \mid H_m, G_h, \sigma) & \text{if } \ H_m > \max \boldsymbol{H}_i, G_h > 0, \ \ \sigma > 0 \\ 0 & \text{else} \end{cases}. \end{aligned} \tag{5}$$

The MCMC chain of H_m, G_h, and σ, which consists of parameter rows sampled from posterior distributions, is obtained by combining the Metropolis–Hastings (MH) method with random walking (Gelman et al., 2013; Hastings, 1970; Kruschke, 2014; Metropolis et al., 1953).

Assuming that the relationships between the carapace length L (L represents the straight carapace length in this study) and age t of sea turtles follow the Bertalanffy equation (Von Bertalanffy, 1938):

$$L(t) = L_m(1 - e^{-G_c t}), \tag{6}$$

where L_m denotes the maximum carapace length, and G_c denotes the growth coefficient of the carapace length. A linear relationship is established between the carapace length L and humeral radius H, as follows:

$$L(H) = C \cdot H, \tag{7}$$

where $C(> 0)$ is the regression coefficient, and the intercept equals 0. Assuming that the carapace data $\boldsymbol{L_j} = (L_1, L_2, \dots, L_j, \dots, L_J)$ (where J denotes the total number of dead individuals corresponding to the humerus radius at death $\boldsymbol{H_j} = (H_1, H_2, \dots, H_j, \dots, H_J)$) follow a normal distribution with a mean of (7) and deviation $\sigma'(> 0)$, the likelihood function of the model can be expressed as follows:

$$f(\boldsymbol{H_j}, \boldsymbol{L_j} \mid C, \sigma') \propto \prod_{j=1}^{J} \frac{1}{\sigma'} \exp\left(-\frac{\{CH_j - L_j\}^2}{2\sigma'^2}\right). \tag{8}$$

Assuming a half-infinite uniform prior distribution for C and σ',

$$\pi(C)\begin{cases} C_c & \text{if } \ C > 0 \\ 0 & \text{else} \end{cases}, \quad \pi(\sigma')\begin{cases} C_{\sigma'} & \text{if } \ \sigma' > 0 \\ 0 & \text{else} \end{cases}, \tag{9}$$

the posterior distribution of the regression coefficient can be obtained as follows:

$$\begin{aligned} p(C, \sigma' \mid \boldsymbol{H_j}, \boldsymbol{L_j}) & \propto p(\boldsymbol{H_j}, \boldsymbol{L_j} \mid C, \sigma') \cdot \pi(C) \cdot \pi(\sigma') \\ & \propto \begin{cases} p(\boldsymbol{H_j}, \boldsymbol{L_j} \mid C, \sigma') & \text{if } \ C > 0, \ \ \sigma' > 0 \\ 0 & \text{else} \end{cases}. \end{aligned} \tag{10}$$

The MCMC chains of C, σ' are obtained using the random walk MH method.

Using (7) and the MCMC chains obtained from (5) and (10), the mean and standard deviation of the maximum humeral radius L_m can be expressed as

$$\mu_{Lm} = \frac{1}{steps} \sum_{i=1}^{steps} H_m^{(i)} \cdot C^{(i)}, \quad \sigma_{Lm} = \sqrt{\frac{1}{steps} \sum_{i=1}^{steps} (H_m^{(i)} \cdot C^{(i)} - \mu_{Lm})^2}, \tag{11}$$

where $steps$ is the number of steps of the MCMC, and (i) denotes the ith chain. In addition, $G_c = G_h$ holds using (1) and (6). Using this equality and the MCMC chains obtained from (5), the mean and deviation of the carapace growth coefficient G_c can be expressed as

$$\mu_{Gc} = \frac{1}{steps} \sum_{i=1}^{steps} G_h^{(i)}, \quad \sigma_{Gc} = \sqrt{\frac{1}{steps} \sum_{i=1}^{steps} (G_h^{(i)} - \mu_{Gh})^2}. \tag{12}$$

Using these means and standard deviations, the prior distributions of L_m and G_c for survival rate estimation are set as follows:

$$\pi(L_m) \propto \frac{1}{\sigma_{Lm}} \exp\left(-\frac{\{L_m - \mu_{Lm}\}^2}{2{\sigma_{Lm}}^2}\right), \quad \pi(G_c) \propto \frac{1}{\sigma_{Gc}} \exp\left(-\frac{\{G_c - \mu_{Gc}\}^2}{2{\sigma_{Gc}}^2}\right). \tag{13}$$

Under these models, the growth curve error can be incorporated into the survival rate estimation as the prior distribution of L_m and G_c.

2.2.2. Construction of an estimator considering immigration

Although the survival rate of loggerhead turtles varies with age and sampling period, few studies have discussed these variations in loggerhead turtle populations in Japan. Therefore, assuming that the survival rate of the loggerhead turtle population is constant, the Malthus model (Malthus, 1798) was used to represent population dynamics. Among the populations represented by the Malthus model, the individuals observed in Japan immigrated to the seas around Japan. Assuming that the migration rate gradually saturates, a logistic model (Pearl and Reed, 1920) was used to represent the immigration rate. Using these assumptions, the observed individuals in Japan N at age t are represented by the product of the Malthus and logistic models:

$$\begin{aligned} N(t) &= N_f e^{-(1-S_r)t} \cdot \frac{1}{1 + e^{-G_v(t - C_v)}} \\ &= N_f \frac{e^{-(1-S_r)t}}{1 + e^{-G_v(t - C_v)}}, \end{aligned} \tag{14}$$

where S_r denotes the population survival rate, G_v denotes the gain of the logistic model, and N_f denotes the population size coefficient (referred to as the size coefficient). C_v indicates the threshold of the logistic model, which is interpreted as the age at which half of the population migrates. If the relationship between the carapace length and age of the sea turtle is expressed by Eq. (6), the age t at carapace length L is expressed as follows:

$$t(L) = -\frac{1}{G_c} \log \frac{L_m - L}{L_m}, \tag{15}$$

where log denotes the natural logarithm. Substituting (15) into (14), the carapace length distribution can be expressed as follows:

$$N(L) = N_f \frac{\left(1 - \frac{L}{L_m}\right)^{\frac{(1-S_r)}{G_c}}}{1 + e^{G_v C_v} \left(1 - \frac{L}{L_m}\right)^{\frac{G_v}{G_c}}}. \tag{16}$$

Assuming that the number of observed individuals $\boldsymbol{N} = (N_1, N_2, \dots, N_k, \dots, N_K)$ (where K denotes the observed number of individuals corresponding to the carapace length $\boldsymbol{L_k} = (L_1, L_2, \dots, L_k, \dots, L_K)$) is sufficiently smaller than the population and using a Poisson distribution with mean $N(L)$, the likelihood function of the model for the carapace length distribution is as follows:

$$f(\boldsymbol{N}, \boldsymbol{L_k} \mid L_m, G_c, G_v, C_v, S_r, N_f) \propto \prod_{k=1}^{K} N(L_k)^{N_k} e^{(-N(L_k))}, \tag{17}$$

where k denotes the carapace length class; in this study, the classes were set at 1 cm intervals. As a prior distribution of the parameters, using (13) for L_m and G_c, the other parameters were set as

$$\pi(G_v)\begin{cases} C_{G_v} & \text{if } \ G_v > 0 \\ 0 & \text{else} \end{cases}, \quad \pi(C_v)\begin{cases} C_{C_v} & \text{if } \ C_v > 0 \\ 0 & \text{else} \end{cases}, \quad \pi(S_r)\begin{cases} C_{S_r} & \text{if } \ S_r > 0 \\ 0 & \text{else} \end{cases}, \quad \pi(N_f)\begin{cases} C_{N_f} & \text{if } \ 0 < N_f \le 1/c_{N_f} \\ 0 & \text{else} \end{cases}. \tag{18}$$

In this study, $1/c_{N_f}$ was set to 100,000 to avoid calculation divergence. In this case, the posterior distribution of the parameters is expressed as

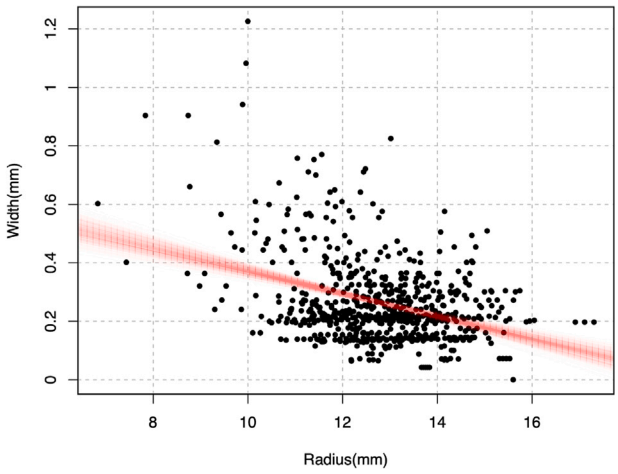

Fig. 1. Model (2) is overlaid on the humerus data with red lines using a set of 1000 parameters of H_m, G_h, σ generated from the posterior distribution (5).

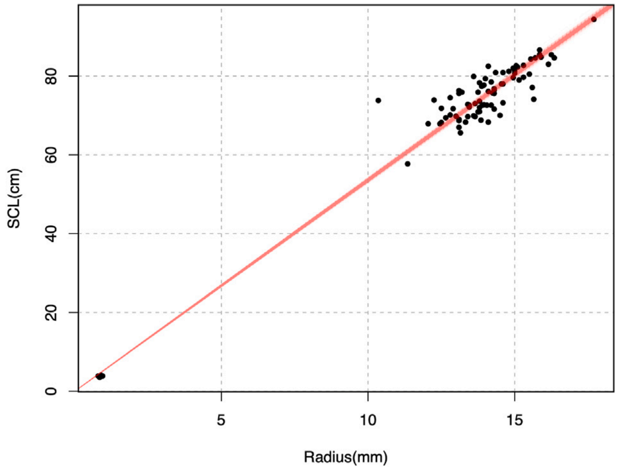

Fig. 2. Model (7) is overlaid on the carapace length and the humerus data with red lines using a set of 1000 parameters of C, σ' generated from the posterior distribution (10).

follows:

$$p(L_m, G_c, G_v, C_v, S_r, N_f \mid \boldsymbol{H_i}, \boldsymbol{H_j}, \boldsymbol{L_j}, \boldsymbol{L_k}, \boldsymbol{\delta H}, \boldsymbol{N})$$
$$\propto f(\boldsymbol{N}, \boldsymbol{L_k} \mid L_m, G_c, G_v, C_v, S_r, N_f)$$
$$\cdot \pi(S_r) \cdot \pi(C_v) \cdot \pi(L_m) \cdot \pi(G_c) \cdot \pi(G_v) \cdot \pi(N_f) \tag{19}$$
$$\propto \begin{cases} f(\boldsymbol{N}, \boldsymbol{L_k} \mid L_m, G_c, G_v, C_v, S_r, N_f) \cdot \pi(L_m) \cdot \pi(G_c). \\ \quad \text{if } G_v > 0, \quad C_v > 0, \quad S_r > 0, \quad 1/c_{N_f} > N_f > 0, \\ 0 \quad \text{else} \end{cases} .$$

The MCMC chains of the parameters were obtained using the Hamiltonian Monte Carlo (HMC) method (Duane et al., 1987; Gelman et al., 2013; Kruschke, 2014) because the random walk MH method is computationally time consuming for this model.

3. Results

The MH and HMC methods were implemented using R (R Core Team, 2021) with an original script (see attached scripts), and MCMC chains $\theta^{(1)}, \theta^{(2)}, \ldots, \theta^{(steps)}$ were obtained, where the number of steps was set to $steps = 5{,}000{,}000$ and the burn-in steps were set to $burnin = 50{,}000$. The chain convergence was assessed based on the plots of the chains (Appendix A: Figures A.1, A.2, and A.3). Using MCMC chains, the posterior means $\sum_{burnin}^{steps} \theta/(steps - burnin)$ were calculated and the 95% HDIs were determined using the *HDInterval* packages (Meredith and Kruschke, 2022).

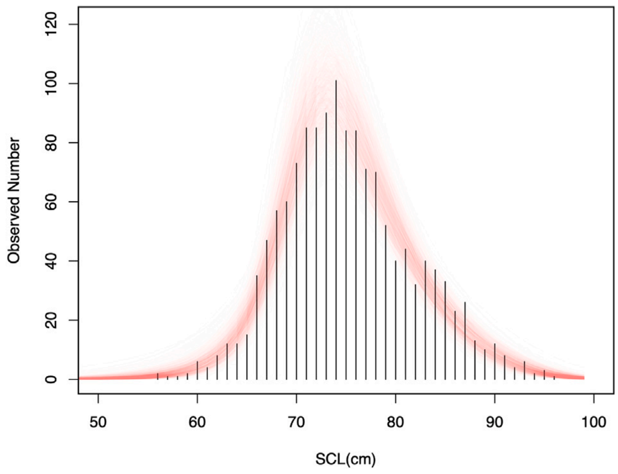

Fig. 3. Model (16) is overlaid on the carapace length distribution with red lines using a set of 1000 parameters of $L_m, G_c, G_v, C_v, S_r, N_f$ generated from the posterior distribution (19).

Table 1
Posterior means and 95% HDIs of parameters obtained by random walk MH method from (5) using humerus radii $\boldsymbol{H_i}$ and LAG widths $\boldsymbol{\delta H}$.

Parameter	95% low	Mean	95% high
Maximum humerus radius H_m (mm)	1.83×10	1.96×10	2.11×10
Growth coefficient G_h (year^{-1})	3.18×10^{-2}	3.98×10^{-2}	4.77×10^{-2}
Standard deviation σ	1.30×10^{-1}	1.37×10^{-1}	1.45×10^{-1}

Table 2
Posterior means and 95% HDIs of parameters obtained by random walk MH method from (10) using humerus radii $\boldsymbol{H_j}$ and carapace length $\boldsymbol{L_j}$.

Parameter	95% low	Mean	95% high
Regression coefficient C	5.30	5.36	5.42
Standard deviation σ'	3.41	4.01	4.64

Table 3
Posterior means and 95% HDIs of parameters obtained by HMC method from (19) using carapace length distribution $\boldsymbol{N}$ corresponding to carapace length $\boldsymbol{L_k}$.

Parameter	95% low	Mean	95% high
Maximum carapace length L_m (cm)	1.00×10^2	1.04×10^2	1.08×10^2
Growth coefficient G_c (year^{-1})	3.61×10^{-2}	3.99×10^{-2}	4.34×10^{-2}
Gain G_v (year^{-1})	4.85×10^{-1}	6.92×10^{-1}	9.16×10^{-1}
Threshold C_v (year)	2.51×10	2.85×10	3.21×10
Survival rate S_r (year^{-1})	7.99×10^{-1}	8.52×10^{-1}	9.03×10^{-1}
Population coefficient N_f	8.20×10^2	1.57×10^4	4.94×10^4

Table 1 lists the posterior means and 95% HDIs of the maximum humeral radius H_m and humerus growth coefficient G_h that were obtained by the random walk MH method from (5) using the humerus radius $\boldsymbol{H_i}$ and LAG width $\boldsymbol{\delta H}$. The parameter estimates were 19.6 mm (95% HDI: 18.3–21.1) for H_m and 0.0398 year^{-1} (95% HDI: 0.0318–0.0477) for G_h. Fig. 1 shows model (2) overlaid with red lines on the humerus data using 1000 sample MCMC chains generated from (5).

Table 2 lists the posterior means and 95% HDIs of the regression coefficient C, as well as the standard deviation σ' obtained by the random walk MH method from (10) using the humerus radius $\boldsymbol{H_j}$ and carapace length $\boldsymbol{L_j}$. C was estimated as 5.36 (95% HDI: 5.30–5.42). Fig. 2 shows model (7) overlaid with red lines on the data of the humeral radius and carapace length using 1000 sample MCMC chains generated from (10).

Table 3 lists the posterior means and 95% HDIs of the maximum carapace length L_m, growth coefficient of the carapace length G_c,

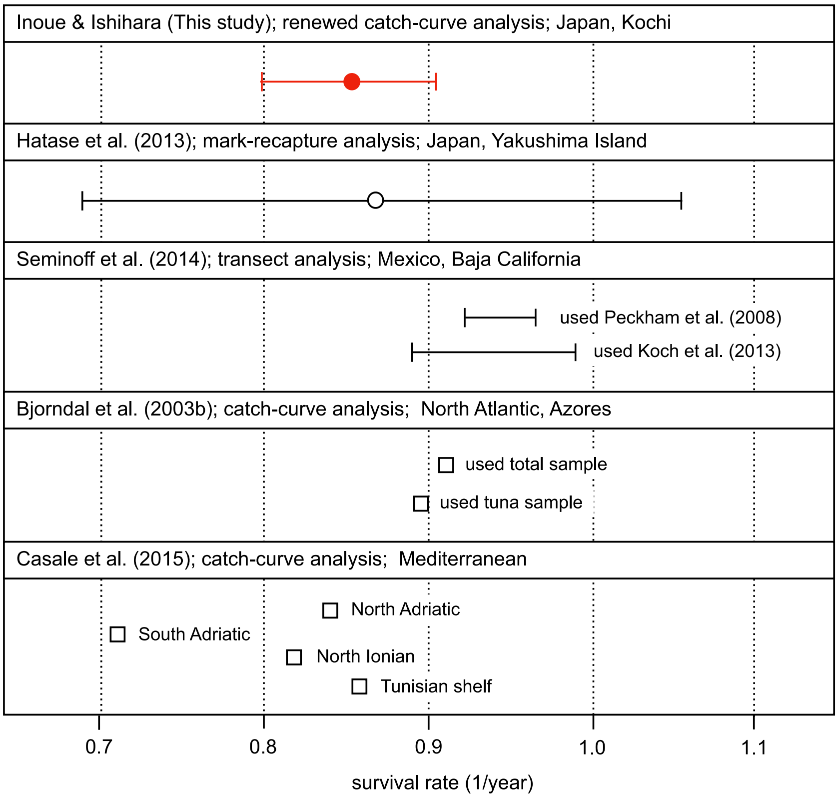

Fig. 4. Comparison of estimated survival rate in various regions. From top to bottom: results of this study, Hatase et al. (2013), Seminoff et al. (2014), Bjorndal et al. (2003b), and Casale et al. (2015).

gain G_v, threshold of the logistic model C_v, survival rate S_r, and size coefficient N_f obtained by the HMC method from (19), using the carapace length distribution $\boldsymbol{N}$ corresponding to the carapace length $\boldsymbol{L}_k$. Important parameter estimates were 0.852 year^{-1} (95% HDI: 0.799–0.903) for S_r and 28.5 years (95% HDI: 25.1–32.1) for C_v. Fig. 3 shows model (16) overlaid with a thin red line on the carapace length distribution data using 1000 sample MCMC chains generated from the posterior distribution (19).

Among the estimated parameters, all except N_f exhibited a symmetric posterior distribution similar to a normal distribution (Appendix A: Figures A.4, A.5, and A.6).

4. Discussion

4.1. Comparison of survival rates

By using a Bayesian approach and improving the model, the survival rate of loggerhead turtles caught as bycatch in Muroto, Kochi Prefecture, Japan was estimated to be 0.852 year^{-1} (95% HDI: 0.799–0.903; Fig. 4). Although a simple comparison is not possible because of the different approaches, it is clear that accuracy and interpretability improved compared to the survival estimates in Japan; that is, 0.871 year^{-1} (95% CI: 0.689–1.053; Fig. 4) (Hatase et al., 2013).

Narrower estimated intervals allowed for comparisons with other regional populations. The results of the line transect analysis for loggerheads along the Baja California coast, namely 0.932–0.965 year^{-1} (using the results of Peckham et al., 2008) and 0.890–0.988 year^{-1} (using the results of Koch et al., 2013) (Seminoff et al., 2014), were slightly higher than our estimates (Fig. 4). As the Japanese loggerhead turtles immigrated from Baja California, the survival rate of the Japanese population was lower than that of the pre-immigration population. This result contrasts our intuition that the older turtles have higher survival rates than the younger turtles, and suggests that mortality factors other than natural mortality affect loggerhead turtles in the waters around Japan.

The results of the catch-curve analysis for immature Atlantic individuals, namely 0.911 year^{-1} (total sample) and 0.894 year^{-1} (tuna sample) (Bjorndal et al., 2003b), were higher than the posterior mean of this study (Fig. 4). These results suggest that the survival rate of larger North Pacific loggerhead turtles may be lower than that of immature Atlantic loggerhead turtles, and the clarification of mortality factors in the population is recommended.

The results of catch-curve analysis performed on individuals of a wide range of ages in the Mediterranean, namely 0.839 year^{-1} (North Adriatic), 0.710 year^{-1} (South Adriatic), 0.817 year^{-1} (North Ionian), and 0.862 year^{-1} (Tunisian shelf) (Casale et al., 2015), were included in the estimation intervals of this study, except for the case of the South Adriatic (Fig. 4). Bycatch is a concern in the Mediterranean (Lazar et al., 2011; Margaritoulis et al., 2003), and a negative effect may exist on a similar level in Japan (Ishihara et al., 2014).

4.2. Comparison of immigration threshold

The threshold of the logistic model C_v, which denotes the age at which half of the loggerhead turtle population immigrated, was estimated to be 28.5 years (95% HDI: 25.1–32.1). Tomaszewicz et al. (2015) estimated the age of the population in the Baja California coastal area using skeletochronology and found that the age distribution decreased from 10 to 24 years. Even considering that the immigration from Baja California to Japan takes one to two years, our estimated C_v is larger than the immigration age assumed from their results.

This suggests that the age estimates in this study may have been overestimated. In the regression growth protocol applied in this study, the growth curve was estimated only by the fit to the LAG width and humeral radius, and the number of LAGs in the individuals was not included in the estimation, which may have caused overestimation (Parham and Zug, 1997). This overestimation can be mitigated by extending the correction factor protocol, which can consider the information of each individual LAG (Parham and Zug, 1997). Because the survival estimates are based on the shape of the carapace length distribution, bias in the age estimates does not significantly affect the survival estimates.

4.3. Overall discussion

Of the four concerns regarding previous catch-curve analysis, namely C1–C4, C1 and C2 were clearly improved. C1 was improved using the result of the growth curve estimation as a prior distribution in the analysis of the carapace length distribution, as shown in Eq. (13). C2 was improved by explicitly considering the immigration in the model, as shown in Eq. (14). C3 did not improve because our approach assumes a constant survival rate and uses the Malthus model in (14). However, this concern can easily be addressed by changing the Malthus model to one in which the survival rate varies with the ages and sizes of the sea turtles. Although C4 is difficult to improve with modeling, it would be possible to discuss the changes in the age distribution over time if data were collected over a long period. The constructed framework allows the survival rate to be estimated with a reduced research time compared to mark-recapture analysis. This study used a carapace length distribution over only approximately seven years. Therefore, it could be easier to evaluate these changes.

The importance of the improvements of C1 and C2 becomes apparent through a comparison with existing catch-curve analyses. In existing methods, linear regression on Eqs. (2) and (7) yields G_h, H_m, and C, which are subsequently used to derive L_m and G_c as $L_m = C \cdot H_m$ and $G_c = C_h$, respectively. Thereafter, the carapace length is converted into age using the Bertalanffy curve (15), and the survival rates are estimated by taking the log linear regression to the latter half of the carapace length distribution beyond its peak (See ExistingMethod.R script in detail). Applying this method to the data in this study produced single survival estimates of 0.872 year^{-1} (See Table A.1 in Appendix A for the other estimated parameters). Figures A.7–9 in Appendix A show the results overlaid with blue lines on the data. Comparing this result with the result of 0.852 year^{-1} (95% HDI: 0.799–0.903) from our method, it is evident that relying solely on a single estimated value that ignores the accumulation of estimation errors is not advisable. This is especially crucial in the construction of conservation plans, where a posterior distribution of the survival rate can present various scenarios. In addition, in existing methods, the absence of limitations from the first half of the carapace length distribution, i.e., the absence of immigration, leads to an overestimation of survival rates compared to our method.

The model proposed in this study is completely novel, and prior knowledge regarding humerus growth marks and survival rates of loggerhead sea turtle populations in Japan is limited. Therefore, biologically limited uniform distributions were used for the prior distributions of H_m, G_h, σ in Eq. (4), C and σ' in Eq. (9), and G_v, C_v, S_r, N_f in Eq. (18). Although the choice of the non-informative prior had little influence on the results of this study, appropriate informative prior distributions can improve the estimation results. Therefore, a clear specification of these prior distributions is expected as new data accumulate, and prior distributions will be updated as the estimations are repeatedly conducted.

The Japanese loggerhead population can be divided into two types of foragers (neritic and oceanic foragers), and these foragers are exposed to different mortality factors (Hatase et al., 2002, 2004, 2010, 2013; Hatase, 2021). Therefore, it is more appropriate to divide the humerus and SCL data into two groups using the isotropic ratio or telomere length (Hatase et al., 2010) and separately estimate the population parameters. Although this grouping may not affect the estimation of immigration thresholds (Hatase et al., 2010), it may affect the estimation of survival rates.

The data sampling methods and sample size can affect survival estimation, but few studies have evaluated their effects on the survival estimation of sea turtles. By using a simulation with the constructed model, we can evaluate these effects and suggest appropriate data sampling methods or sample sizes for reliable survival comparison (Inoue unpublished).

In the future, accumulating landing and stranding data may enable us to estimate and compare the survival rates of subpopulations in Japan. In addition to this survival estimation, information regarding habitat areas, types of fisheries, and number of days in operation can help us to identify population decline factors. For this purpose, it is appropriate to extend our model to a hierarchical form to incorporate this information as explanatory variables.

CRediT authorship contribution statement

Naoto K. Inoue: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Formal analysis, Data curation, Conceptualization. **Takashi Ishihara:** Writing – review & editing, Resources, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are already published and publicly available. Programs and sample data are provided at https://github.com/naoto4696/SurvivalEstimation-SeaTurtles.git.

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Appendix A. Supplementary data

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References

Allen, K.R., 1966. A method of fitting growth curves of the von bertalanffy type to observed data. J. Fish. Res. Board Can. 23, 163–179. http://dx.doi.org/10.1139/f66-016.

Avens, L., Goshe, L.R., Coggins, L., Snover, M.L., Pajuelo, M., Bjorndal, K.A., Bolten, A.B., 2015. Age and size at maturation-and adult-stage duration for loggerhead sea turtles in the western North Atlantic. Mar. Biol. 162, 1749–1767. http://dx.doi.org/10.1007/s00227-015-2705-x.

Avens, L., Goshe, L.R., Pajuelo, M., Bjorndal, K.A., MacDonald, B.D., Lemons, G.E., . . ., J.A., 2013. Complementary skeletochronology and stable isotope analyses offer new insight into juvenile loggerhead sea turtle oceanic stage duration and growth dynamics. Mar. Ecol. Prog. Ser. 491, 235–251. http://dx.doi.org/10.3354/meps10454.

Barker, R.J., 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. Biometrics 53 (2), 666–677. http://dx.doi.org/10.2307/2533966.

Bjorndal, K.A., Bolten, A.B., Dellinger, T., Delgado, C., Martins, H.R., 2003a. Compensatory growth in oceanic loggerhead sea turtles: response to a stochastic environment. Ecology 84 (5), 1237–1249. http://dx.doi.org/10.1890/0012-9658(2003)084[1237,CGIOLS]2.0.CO;2.

Bjorndal, K.A., Bolten, A.B., Martins, H.R., 2003b. Estimates of survival probabilities for oceanic-stage loggerhead sea turtles (Caretta caretta) in the North Atlantic. Fish. Bull. 101 (4), 732–737, http://hdl.handle.net/1834/31016.

BraunMcNeill, J., Sasso, C.R., Avens, L., 2007. Estimates of realized survival for juvenile loggerhead sea turtles (Caretta caretta) in the United States. Herpetol. Conserv. Biol. 2 (2), 100–105.

Casale, P., Conte, N., Freggi, D., Cioni, C., Argano, R., 2011. Age and growth determination by skeletochronology in loggerhead sea turtles(Caretta caretta) from the Mediterranean Sea. Sci. Mar.(Barcelona) 75 (1), 197–203, http://digital.casalini.it/2478336.

Casale, P., Freggi, D., Furii, G., Vallini, C., Salvemini, P., Deflorio, M., . . ., B.J., 2015. Annual survival probabilities of juvenile loggerhead sea turtles indicate high anthropogenic impact on Mediterranean populations. Aquat. Conserv. Mar. Freshw. Ecosyst. 25 (5), 690–700. http://dx.doi.org/10.1002/aqc.2467.

Casale, P., Mazaris, A.D., Freggi, D., Basso, R., Argano, R., 2007. Survival probabilities of loggerhead sea turtles (Caretta caretta) estimated from capture-mark-recapture data in the Mediterranean Sea. Sci. Mar. 71 (2), 365–372. http://dx.doi.org/10.3989/scimar.2007.71n2365.

Caswell, H., 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81 (3), 619–627. http://dx.doi.org/10.1890/0012-9658(2000)081[0619,PARPAT]2.0.CO;2.

Chaloupka, M., Limpus, C., 2002. Survival probability estimates for the endangered loggerhead sea turtle resident in southern Great Barrier Reef waters. Mar. Biol. 140, 267–277. http://dx.doi.org/10.1073/pnas.6.6.275.

Duane, S., Kennedy, A.D., Pendleton, B.J., Roweth, D., 1987. Hybrid Monte Carlo. Phys. Lett. B 195 (2), 216–222. http://dx.doi.org/10.1016/0370-2693(87)91197-X.

Frazer, N.B., 1987. Preliminary estimates of survivorship for wild juvenile loggerhead sea turtles (Caretta caretta). J. Herpetol. 21 (3), 232–235. http://dx.doi.org/10.2307/1564489.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., Rubin, D.B., 2013. Bayesian Data Analysis. Chapman and Hall/CRC.

Guarino, F.M., Nocera, F.Di., Pollaro, F., Galiero, G., Iaccarino, D., Iovino, D., . . ., Maio, N., 2020. Skeletochronology, age at maturity and cause of mortality of loggerhead sea turtles Caretta caretta stranded along the beaches of Campania (south-western Italy, western Mediterranean Sea). Herpetozoa 33, 39–51. http://dx.doi.org/10.3897/herpetozoa.33.e47543.

Hastings, W.K., 1970. Monte Carlo sampling methods using Markov chains and their applications. Biometrika 57 (1), 97–109. http://dx.doi.org/10.1093/biomet/57.1.97.

Hatase, H., 2021. Mechanisms that produce and maintain a foraging dichotomy in adult loggerhead turtles (Caretta caretta) Which tactic has higher fitness, oceanic or neritic? J. Exp. Mar. Biol. Ecol. 541, 151586. http://dx.doi.org/10.1016/j.jembe.2021.151586.

Hatase, H., Goto, K., Sato, K., Bando, T., Matsuzawa, Y., Sakamoto, W., 2002. Using annual body size fluctuations to explore potential causes for the decline in a nesting population of the loggerhead turtle Caretta caretta at Senri Beach, Japan. Mar. Ecol. Prog. Ser. 245, 299–304. http://dx.doi.org/10.3354/meps245299.

Hatase, H., Matsuzawa, Y., Sato, K., Bando, T., Goto, K., 2004. Remigration and growth of loggerhead turtles (Caretta caretta) nesting on Senri Beach in Minabe, Japan: life-history polymorphism in a sea turtle population. Mar. Biol. 144, 807–811. http://dx.doi.org/10.1007/s00227-003-1232-3.

Hatase, H., Omuta, K., Tsukamoto, K., 2010. Oceanic residents, neritic migrants: a possible mechanism underlying foraging dichotomy in adult female loggerhead turtles (Caretta caretta). Mar. Biol. 157, 1337–1342. http://dx.doi.org/10.1007/s00227-010-1413-9.

Hatase, H., Omuta, K., Tsukamoto, K., 2013. A mechanism that maintains alternative life histories in a loggerhead sea turtle population. Ecology 94 (11), 2583–2594. http://dx.doi.org/10.1890/12-1588.1.

Ishihara, T., 2011. Life History in Maturation Process of Loggerhead Turtles (Caretta Caretta) in North Pacific. University of Tokyo.

Ishihara, T., Kamezaki, N., Matsuzawa, Y., Ishizaki, A., 2014. Assessing the status of Japanese coastal fisheries and sea turtle bycatch. Wildl. Hum. Soc. 2, 23–35. http://dx.doi.org/10.20798/awhswhs.2.1_23.

Ishihara, T., Kamezaki, N., Matsuzawa, Y., Iwamoto, F., Oshika, T., Miyagata, Y., . . ., Yamashita, S., 2011. Reentery of juvenile and sub-adult loggerhead turtles into natal waters of Japan. Curr. Herpetol. 30 (1), 63–68. http://dx.doi.org/10.5358/hsj.30.63.

IUCN, 2022. The IUCN red list of threatened species version 2022-2. https://www.iucnredlist.org.

Kamezaki, N.I., Matsuzawa, Y., Abe, O., Asakawa, H., Fujii, T., Goto, K., Hagino, S., Hayami, M., Ishii, M., Iwamoto, T., Kamata, T., Kato, H., Kodama, J., Kondo, Y., Miyawaki, I., Mizobuchi, K., Nakamura, Y., Nakashima, Y., Naruse, H., Omuta, K., Samejima, M., Suganuma, H., Takeshita, H., Tanaka, T., Toji, T., Uematsu, M., Yamamoto, A., Yamato, T., Wakabayashi, I., 2003. Loggerhead turtles nesting in Japan. In: Bolten, A.B., Witherington, B.E. (Eds.), Loggerhead Sea Turtles. Smithsonian Institution Press, Washington, DC, USA, pp. 210–217.

Kendall, W.L., 2004. Coping with unobservable and mis–classified states in capture–recapture studies. Anim. Biodivers. Conserv. 27 (1), 97–107.

Koch, V., Peckham, H., Mancini, A., Eguchi, T., 2013. Estimating at-sea mortality of marine turtles from stranding frequencies and drifter experiments. PLoS One 8 (2), e56776. http://dx.doi.org/10.1371/journal.pone.0056776.

Kruschke, J., 2014. Doing Bayesian Data Analysis: A Tutorial with R. JAGS, and Stan.

Lazar, B., Maslov, L., Romanić, S.H., Gračan, R., Krauthacker, B., Holcer, D., Tvrtković, N., 2011. Accumulation of organochlorine contaminants in loggerhead sea turtles, Caretta caretta, from the eastern Adriatic Sea. Chemosphere 82 (1), 121–129. http://dx.doi.org/10.1016/j.chemosphere.2010.09.015.

Lenz, A.J., Avens, L., Campos Trigo, C., Borges-Martins, M., 2016. Skeletochronological estimation of age and growth of loggerhead sea turtles (Caretta caretta) in the western South Atlantic Ocean. Austral Ecol. 41 (5), 580–590. http://dx.doi.org/10.1111/aec.12347.

Malthus, T.R., 1798. An essay on the principle of population.

Margaritoulis, D., Argano, R., Baran, I., Bentivegna, F., Bradai, M.N., Camiñas, J.A., . . ., Lazar, B., 2003. Loggerhead turtles in the Mediterranean: present knowledge and conservation perspectives. In: Bolten, A.B., Witherington, B.E. (Eds.), Loggerhead Sea Turtles. Smithsonian Institution Press, Washington, DC, USA, pp. 175–198.

Matsuzawa, Y., Kamezaki, N., Ishihara, T., Omuta, K., Takeshita, H., Goto, K., . . ., P.H., 2016. Fine-scale genetic population structure of loggerhead turtles in the Northwest Pacific. Endanger. Species Res. 30, 83–93. http://dx.doi.org/10.3354/esr00724.

McCarthy, M.A., 2007. Bayesian Methods for Ecology. Cambridge University Press.

Meredith, M., Kruschke, J., 2022. HDInterval: Highest (posterior) density intervals. https://CRAN.R-project.org/package=HDInterval, R package version 0.2.4.

Metropolis, N., Rosenbluth, A.W., Rosenbluth, M.N., Teller, A.H., Teller, E., 1953. Equation of state calculations by fast computing machines. J. Chem. Phys. 21 (6), 1087–1092. http://dx.doi.org/10.1063/1.1699114.

Monk, M.H., Berkson, J., Rivalan, P., 2011. Estimating demographic parameters for loggerhead sea turtles using mark–recapture data and a multistate model. Popul. Ecol. 53, 165–174. http://dx.doi.org/10.1007/s10144-010-0205-x.

Parham, J.F., Zug, G.R., 1997. Age and growth of loggerhead sea turtles (Caretta caretta) of coastal Georgia: an assessment of skeletochronological age-estimates. Bull. Mar. Sci. 61 (2), 287–304.

Pearl, R., Reed, L.J., 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. Proc. Natl. Acad. Sci. 6 (6), 275–288. http://dx.doi.org/10.1073/pnas.6.6.275.

Peckham, S.H., Maldonado-Diaz, D., Koch, V., Mancini, A., Gaos, A., Tinker, M.T., Nichols, W.J., 2008. High mortality of loggerhead turtles due to bycatch, human consumption and strandings at Baja California Sur, Mexico, 2003 to 2007. Endanger. Species Res. 5 (2–3), 171–183. http://dx.doi.org/10.3354/esr00123.

Petitet, R., Secchi, E.R., Avens, L., Kinas, P.G., 2012. Age and growth of loggerhead sea turtles in southern Brazil. Mar. Ecol. Prog. Ser. 456, 255–268. http://dx.doi.org/10.3354/meps09681.

Phillips, K.F., Mansfield, K.L., Die, D.J., Addison, D.S., 2014. Survival and remigration probabilities for loggerhead turtles (Caretta caretta) nesting in the eastern Gulf of Mexico. Mar. Biol. 161, 863–870. http://dx.doi.org/10.1007/s00227-013-2386-2.

Piovano, S., Clusa, M., Carreras, C., Giacoma, C., Pascual, M., Cardona, L., 2011. Different growth rates between loggerhead sea turtles (Caretta caretta) of Mediterranean and Atlantic origin in the Mediterranean Sea. Mar. Biol. 158, 2577–2587. http://dx.doi.org/10.1007/s00227-011-1759-7.

Pradel, R., Hines, J.E., Lebreton, J.D., Nichols, J.D., 1997. Capture-recapture survival models taking account of transients. Biometrics 53 (1), 60–72. http://dx.doi.org/10.2307/2533097.

R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/.

Ramirez, M.D., Avens, L., Seminoff, J.A., Goshe, L.R., Heppell, S.S., 2017. Growth dynamics of juvenile loggerhead sea turtles undergoing an ontogenetic habitat shift. Oecologia 183, 1087–1099. http://dx.doi.org/10.1007/s00442-017-3832-5.

Sasso, C.R., Braun-McNeill, J., Avens, L., Epperly, S.P., 2006. Effects of transients on estimating survival and population growth in juvenile loggerhead turtles. Mar. Ecol. Prog. Ser. 324, 287–292. http://dx.doi.org/10.3354/meps324287.

Sea turtle conference in Japan, 2007. Sea turtle conservation handbook. https://www.env.go.jp/content/900491148.pdf.

Seminoff, J.A., Eguchi, T., Carretta, J., Allen, C.D., Prosperi, D., Rangel, R., . . ., Peckham, S.H., 2014. Loggerhead sea turtle abundance at a foraging hotspot in the eastern Pacific Ocean: implications for at-sea conservation. Endanger. Species Res. 24 (3), 207–220. http://dx.doi.org/10.3354/esr00601.

Snover, M.L., Hohn, A.A., Crowder, L.B., Macko, S.A., 2010. Combining stable isotopes and skeletal growth marks to detect habitat shifts in juvenile loggerhead sea turtles Caretta caretta. Endanger. Species Res. 13 (1), 25–31. http://dx.doi.org/10.3354/esr00311.

Tomaszewicz, C.N.T., Seminoff, J.A., Avens, L., Goshe, L.R., Peckham, S.H., Rguez-Baron, J.M., . . ., Kurle, C.M., 2015. Age and residency duration of loggerhead turtles at a North Pacific bycatch hotspot using skeletochronology. Biol. Cons. 186, 134–142. http://dx.doi.org/10.1016/j.biocon.2015.03.015.

Von Bertalanffy, L., 1938. A quantitative theory of organic growth (inquiries on growth laws, II). Hum. Biol. 10 (2), 181–213, https://www.jstor.org/stable/41447359.

Zug, G.R., Wynn, A.H., Ruckdeschel, C., 1986. Age determination of loggerhead sea turtles, Caretta caretta, by incremental growth marks in the skeleton. Smithson. Contrib. Zool. 427, 1–34.