

ARTICLE

Estimating Growth of Caribbean Spiny Lobster Using Mark–Recapture Data

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Abstract

To estimate the growth of the hard-to-age Caribbean spiny lobster *Panulirus argus* in the southeastern USA, a double-maximum-likelihood-estimation method (referred to as the “likelihood model”) has been applied to the mark–recapture data collected in the Florida Keys from 1967 to 2003. Parameters related to the intermolt period and the growth increment have been assessed, and the uncertainty of the parameters has been estimated using the bootstrap resampling method. For better comparison with the previously published step-wise growth models, an individual-based model, in which the variance and covariance of model parameters were fully considered, has been developed to simulate growth transition matrices. The simulation results were compared directly by using the Frobenius Norm. The results indicated that the likelihood model produces a more conservative growth estimate with lower uncertainty. However, the likelihood weights should be set with caution. This study can improve our understanding of the growth of the Caribbean spiny lobster. The products can be directly used in the future for integrated size-structured, stock assessment models for Caribbean spiny lobster; the methods can be easily adaptable to other crustacean species.

The Caribbean spiny lobster *Panulirus argus* is widely distributed in tropical and subtropical waters of the Atlantic Ocean (Phillips and McWilliam 1986; De León et al. 2005; Freitas and Castro 2005; Rudorff et al. 2009). This species is harvested by 23 counties in the Caribbean area and supports the most valuable fisheries in the region (Holthuis 1991; Ehrhardt 2001; Heileman 2007). Due to its economic importance, various stock assessment models have been produced to describe the population dynamics of the Caribbean spiny lobster, including virtual population analysis (Gongora 2010), a yield-per-recruit model (Font 2002; Fadrugas 2005), the state–space model, statistical catch-at-age analysis, and the modified DeLury

model (SEDAR 2010). However, none of above models accounted for variability in growth.

Modeling the growth of individuals of a species is an essential component in stock assessment, as that relates to the expected growth of a fishery stock, which directly affects the sustainable harvest level (Holland 2010; Francis 2016). Traditional spiny lobster stock assessment models are stage- or age-structured and use continuous growth curves, e.g., von Bertalanffy growth functions (Fadrugas 2005; Gongora 2010; SEDAR 2010). However, the unique life history of the Caribbean spiny lobster makes its growth hard to formulate. First, the growth of a Caribbean spiny lobster individual is discontinuous. The lobster’s size only

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changes as a result of the molting process; otherwise, it remains unchanged during the intermolt period. This growth pattern is called “stepwise growth” (Anger 1998). Second, the Caribbean spiny lobster lacks otoliths, vertebrae, and scales that are found in finfish species and used to help estimate age. Last but not least, significant variations exist in the growths of individual lobsters within a stock and among stocks (FAO 2001). Newly emerged aging methods include taking measurements of the pigment neurolipofuscin (Maxwell et al. 2007) or the eyestalk, or by examining the gastric mill (Kilada et al. 2012). However, until now those methods have not been proven to be precise enough to represent the growth of Caribbean spiny lobster. Because of those biological features described above, caution should be exercised when traditional continuous growth models are employed to describe the step-wise growth process. Applying mark–recapture data in continuous growth model-fitting could introduce bias and amplify uncertainty, as the observed size change and the recorded period at liberty are asynchronous. Furthermore, a deficiency of von Bertalanffy growth functions is that the maximum size and growth rate parameters are negatively correlated (Pardo et al. 2013; Johnson and Swenarton 2016). For species like lobster, whose maxima are always unknown, combination assumptions need to be made on the growth parameters. For example, Punt et al. (2006) assumed one parameter to be fixed for the population, while allowing the other to vary among individuals. Besides the physiological constraints, e.g., younger lobsters molt more frequently than elders (Ehrhardt 2008), some environmental factors may also affect the molting frequency of the lobster, such as abundance of food and water temperature (Lellis and Russell 1990). In addition, the average growth of the carapace length (CL) per molt varies between sexes (female and male) and seasons (summer and winter) for Caribbean spiny lobster (Ehrhardt 2008).

Fisheries scientists have investigated the growth of the Caribbean spiny lobster based on its molting process. Hoenig and Restrepo (1989) developed a “molt–no-molt” model to estimate the probability of molting according to the intermolt period and the “days-free” (number of days between the release and recapture dates). The duration of the intermolt period was also assumed to be an exponential function of the CL at the time of tagging. Based on comparison of the recorded days-free with the estimated inter-molt period, each recapture record is classified into one of three types—no molt, molt once by chance, and molt at least once—with the probability of that outcome calculated using the days-free and estimated intermolt period. The total likelihood is the product of the probability that each recorded individual falls into one of the above three types. Consequently, parameters could be estimated by maximizing the total likelihood. However, lobsters with unchanged CL had been observed after a long days-free period but were not included

in Hoenig and Restrepo (1989), and the molting increment was not estimated either. Muller et al. (1997) used hierarchical generalized linear models (GLMs) to describe the growth procedure of the lobster in two processes: molting probability and molting increment. The probability that an individual lobster molts in a given month was linked to a logit function of its CL at tagging time and days-free, as well as zone (using Big Pine Key as the boundary between the upper and lower Florida Keys, hereafter Keys), season (summer from May to October or winter from November to the next April), and sex (female or male). For the growth increment, a log-normal error distribution was assumed with an identity link function, and the CL, days-free, season, zone, and sex were also considered. Ehrhardt (2008) described another Caribbean spiny lobster growth model that was originated from Munro (1974). Two regressions were used. Observation records were delivered into a set of predefined CL bins on the basis of the CL at time of tagging. The median intermolt period was roughly estimated according to the cumulative percentage of molted individuals against the days-free, and an exponential function was used to explore the relationship between the median intermolt periods and the median size of those bins (Munro 1974). Then a linear function was taken to fit the premolt and postmolt CLs. Sex (female and male) and CL (<70 and >70 mm) were considered to yield the growth differences.

Both Hoenig and Restrepo (1989) and Muller et al. (1997) used mark–recapture data as their only data source. Mark–recapture data is a primary information source that uses a probabilistic framework to estimate the growth rates of aquatic species (Laslett et al. 2002), especially for those species for which aging methods cannot be implemented directly (Wang et al. 1995). Marking and recapturing organisms from a natural population instead of experimental environments could reduce bias caused by controlled experimental settings and produce greater accuracy in prediction. Ehrhardt (2008) used mark–recapture data as well but included some laboratory observations from Sweat (1968) to investigate the intermolt period of young lobsters. To separate single-molt individuals from those with multiple molts, Muller et al. (1997) set a 4-month (120 d) cut-off value for days-free.

Previous studies about the growth of Caribbean spiny lobster individuals only focused on developing deterministic equations but failed to encompass the uncertainty of the parameters. With the growth curves, the catch-at-length data can be transformed into catch-at-age data that are required by the age-structured stock assessment model (Muller et al. 1997; SEDAR 2010). For example, the latest stock assessment adopted the mean growth curves of Ehrhardt (2008), but no relevant justification was provided for the one-to-one corresponding age–length key (SEDAR 2010). However, being an important source of uncertainty for population dynamics, variations in the

growth of the lobsters should not be ignored in stock assessment.

The main objective of this study was to develop growth transition matrices for the Caribbean spiny lobster in Florida waters from the mark-recapture data. A statistical model that originated from Hoenig and Restrepo (1989) was modified. Then the results of the newly developed method were compared with those derived from previously published step-wise growth models that had been applied to describe the growth of Caribbean spiny lobster, such as in Muller et al. (1997) and Ehrhardt (2008). The growth transition matrices, which indicate the percentage of individuals in each size bin that remain in the same bin or molt into larger size bins in one time-step (e.g., a season), could be simulated and compared. The most accurate and precise ones would be identified and recommended for the future, "integrated," size-structured, stock assessments. This study could promote our understanding of the growth of the Caribbean spiny lobster and will be easily adaptable to other crustacean species.

METHODS

Mark-recapture data.—The Florida Fish and Wildlife Commission (FLFWC) provided the mark-recapture data that we used in this project. The data were collated from long-term tagging experiments conducted from 1967 to 2003, and the mark-recapture methods were consistent throughout the decades (Hunt and Lyons 1986; Muller et al. 1997; Ehrhardt 2008). In total, 6,967 individual lobsters with tags were recaptured; 6,469 (92.8%) were tagged from 1975 to 1979, 118 (nearly 2%) lobsters were tagged before 1970, and 380 (>5%) lobsters were tagged after 1998. For most recaptured lobsters, their length at tagging, recapture length, and days-free were recorded, as well as sex, injury (whether the lobster was missing a limb), tagging season, tagging zone, and tagging area (bayside or ocean side of the Keys). Records with missing information on either tagging or recapture length were excluded for the purpose of growth modeling. After data filtering, 6,891 records remained. Most of the data collected in the lower Keys were collected from June 1975 to October 1976, which accounts for 46.2% of the total data, while the remaining 53.8% of the data were collected in the upper Keys from January 1978 to March 1979 (Muller et al. 1997). In the data collection, the measurement error was suggested as 2 mm CL, which means only those recaptured individuals with more than 2-mm increases in CL were considered as molted lobsters (Hunt and Lyons 1986; Ehrhardt 2008). Other lobsters that may have molted but without a detectible increase in size (Marshall 1948) were treated as nonmolted individuals. It is a reasonable modeling assumption, as the main objective of this study was to develop growth transition matrices for future size-structured stock assessments, and those

lobsters that molt without a size change do not contribute to the growth of the stock.

After 1967, 5,505 (~80%) lobsters without a change in size were recaptured, while 1,386 (~20%) of the tagged lobsters molted and had at least a 2-mm increment in CL. For the rest of the tagged lobsters, growth information was missing. From the valid growth records, the average days-free was 23.33 d, 4,622 (~67%) individuals were tagged in summer, 3,704 (~54%) individuals were tagged in the upper Keys, 3,971 (~58%) lobsters were tagged from the bay side, 51% of the tagged samples were female, and the injury rate of the tagged lobsters was 25%. The size distribution of the tagged lobster population was 73.78 ± 11.27 mm CL (mean \pm SD), and that of the recaptured population was 75.26 ± 11.26 mm CL.

Permutation tests based on 10,000 resampling iterations are used to compare data between sexes, tagging seasons, tagging areas, tagging zones, injury categories, and time periods (before 1980 and after 1998). For example, by randomly shuffling the observed sex, the permuted growth difference can be calculated. Considering growth as universal between sexes, reassigning sex should not affect the mean appreciably. Then the rank of the observed growth difference among the permuted growth difference distributions gives a *P*-value (Good 1994).

Statistical analyses.—According to Hoenig and Restrepo (1989), for the individual *i*, the "elapsed time" since the last molt to the date of tagging is assumed to be uniformly distributed between 0 and $g(CL_i)$. Here $g()$ is a sex-specific exponential function describing the intermolt period at the length CL_i :

$$g(CL_i) = \begin{cases} a_f e^{b_f CL_i} & \text{for female} \\ a_m e^{b_m CL_i} & \text{for male} \end{cases}, \quad (1)$$

where a_f and b_f and a_m and b_m are sets of parameters for females (*f*) and males (*m*), respectively. By comparing Δt_i and $g(CL_i)$, the mark-recapture records can be classified into four categories:

$$\text{Category 1:} \quad \text{if } \Delta t_i < g(CL_i), \quad P_i^1 = \frac{\Delta t_i}{g(CL_i)};$$

$$\text{Category 2:} \quad \text{if } \Delta t_i < g(CL_i), \quad P_i^2 = 1 - \frac{\Delta t_i}{g(CL_i)};$$

$$\text{Category 3:} \quad \text{if } \Delta t_i \geq g(CL_i), \quad P_i^3 = 1;$$

and

$$\text{Category 4:} \quad \text{if } \Delta t_i \geq g(CL_i), \quad P_i^4 = e^{-20}.$$

Category 1 represents all lobsters that molt by chance (the change in CL is ≥ 2 mm, and days-free is less than the

expected intermolt period). Category 2 represents lobsters that have not molted (the change in CL is <2 mm, and days-free is less than the expected intermolt period). When Δt_i is greater than or equal to the expected intermolt period, lobsters should molt (the change in CL is ≥ 2 mm) and have a theoretical 100% molting probability, which classifies them as category 3. Detailed explanations about the probability that records fall into each category can be found in Hoenig and Restrepo (1989). A new category (category 4) is added to allow for lobsters having a long days-free and unchanged CL (the change in CL is <2 mm, and days-free is greater than or equal to the expected intermolt period), and a penalty weight is set to minimize the negative log likelihood, i.e., e^{-20} . The total likelihood that all marked and recaptured lobsters fall into the four categories can be constructed and maximized for parameter estimation by multiplying likelihood of all individuals:

$$L_{molt} = \prod_{i=1}^{n_1} \left[\frac{\Delta t_i}{g(CL_i)} \right] \prod_{i=1}^{n_2} \left[1 - \frac{\Delta t_i}{g(CL_i)} \right] \prod_{i=1}^{n_3} (1) \prod_{i=1}^{n_4} (e^{-20}). \tag{2}$$

Here, n_1 , n_2 , n_3 , and n_4 are the number of individuals that fall into categories 1 through 4, respectively.

To prevent overestimation of the molting increment, multiple-molt individuals that molt multiple times need to be distinguished from single-molt lobsters (Hoenig and Restrepo 1989). For each of the category 3 individuals, probabilities that the individual falls into two subcategories are calculated as follows:

$$\text{Category 3.1: } P_i^{*,3.1} = 1 - \frac{\Delta t_i - g(CL_i^*)}{g(CL_i)}$$

and

$$\text{Category 3.2: } P_i^{*,3.2} = \frac{\Delta t_i - g(CL_i^*)}{g(CL_i)},$$

where $P_i^{*,3.1}$ is the probability that individual i has only one molt, and $P_i^{*,3.2}$ is the molting probability of the individual i having another molt before the recapture date, conditional on already having one molt. The parameter CL_i^* is the post-CL of lobster i after one molt. Although the exact length is unknown, its range lies between CL_i and the length at recapture. Based on the estimated parameters in $g(CL_i)$, an estimate can be made for the range of the next intermolt period after tagging, $g(CL_i^*)$. Then the Naïve Bayes Rule (Ye et al. 2011) is adopted in the classification: when $P_i^{*,3.1} > P_i^{*,3.2}$, which means $\Delta t_i < 0.5g(CL_i) + g(CL_i^*)$, an individual lobster would have higher possibility to molt only once; otherwise, multiple molts would be more likely to occur. According to the estimate of $g(CL_i^*)$, most of $P_i^{*,3.1}$ and $P_i^{*,3.2}$ could be roughly compared due with their nonoverlapping ranges. Only a few molting records will be excluded, as

the times of molting are difficult to determine. A lognormal error distribution is assumed for the molting increment, ΔCL_i , and a linear relationship is detected between the logarithmic molting increment and the tagging length:

$$\log(\Delta CL_i) = \begin{cases} c_f CL_i + d_f & \text{for female} \\ c_m CL_i + d_m & \text{for male} \end{cases}, \tag{3}$$

where c_f and d_f and c_m and d_m are parameter sets for females and males, respectively. Therefore, the likelihood of the molting increment can be estimated as

$$L_{inc} = \prod_{i=1}^{n_{om}} \left[\frac{1}{\sqrt{2\pi}\sigma_i(CL_i^* - CL_i)} e^{-\frac{(\log(CL_i^* - CL_i) - \log(\Delta CL_i))^2}{2\sigma_i^2}} \right], \tag{4}$$

where n_{om} is the number of the single-molt lobsters, and σ_i is the specified SD of the molting increment, which is assumed to vary exponentially among individuals:

$$\sigma_i = \begin{cases} e^{\phi_f CL_i + \psi_f} & \text{for female} \\ e^{\phi_m CL_i + \psi_m} & \text{for male} \end{cases}. \tag{5}$$

The growth increment parameters, ϕ_f , ψ_f , ϕ_m , and ψ_m can be estimated by maximizing L_{inc} . As the total likelihood is a combination of equations (2) and (5), this method is referred to as the likelihood model in the following comparison.

The uncertainty of parameters, including variances and covariance, are estimated by using a bootstrap method, one of the commonly used resampling techniques to estimate statistical relationships of parameters without strong parametric assumptions to diagnose estimator bias (Magnusson et al. 2013). This technique has been widely used to estimate error structures in fisheries surveys (Smith and Gavaris 1993; Smith 1997). In each resampling, 100% of the records are randomly selected with replacement from the original data pool to estimate model parameters. The resampling process is repeated 10,000 times for each statistical model, with the purpose of obtaining stable parameters, and then the distributions of the model parameters can be determined without making strong parametric assumptions (Efron and Tibshirani 1993).

Previous methods.—In the method from Muller et al. (1997), when the molting probability of individual i , P_i , is estimated at the recapture date, a logit link function is adopted with the assumption that the error follows a binomial distribution:

$$P_i = \frac{e^{a+bCL_i+c\Delta t_i+dZ_i+eT_i+gX_i}}{1 + e^{a+bCL_i+c\Delta t_i+dZ_i+eT_i+gX_i}} \tag{6}$$

where a is a constant, b is the coefficient for tag carapace length, CL_i , c is the coefficient for days-free, Δt_i , d is the coefficient for tagging zone, Z_i , e is the coefficient for

tagging season, T_i , and g is the coefficient for sex, X_i . For the individual i , whose molting probability is predicted to be greater than 0.5, its molting increment, I_i (mm), can be fitted by an exponential function:

$$I_i = e^{\tilde{a} + \tilde{b}CL_i + \tilde{c}\Delta t_i + \tilde{d}Z_i + \tilde{e}T_i + \tilde{g}X_i}, \quad (7)$$

where parameters \tilde{a} to \tilde{g} have the same biological meanings as parameters a to g , but the values are not constrained to be the same. The molting increment error is assumed to be lognormally distributed. We refer to this method as the “generalized regression model” in our analysis.

Although lacking laboratory data from Sweat (1968), the method from Ehrhardt (2008) and Munro (1974) is repeated and referred to as the “double regression model” in our analysis. The individuals with a length at tagging larger than 40 mm CL are first classified into sex-specific, 5-mm-interval size bins, and subsequently sorted in an ascending order within each size bin according to their days-free. A regression is conducted to fit the cumulative percentage that the lobsters molt in each size bin along an increasing days-free period to the cumulative normal distribution (Munro 1974). The median days-free (when 50% of the lobsters molt) of the size bin is estimated from the regression. Similar to Munro (1974) and Hoenig and Restrepo (1989), tagging is assumed to randomly occur between 0 and the full intermolt period. Therefore, the intermolt period, on average, should be twice that the estimated median days-free (Ehrhardt 2008). An exponential relationship is also assumed between the average intermolt period and the corresponding average tagging length:

$$g(CL_i) = \begin{cases} e_f e^{g_f CL_i} & \text{for female} \\ e_m e^{g_m CL_i} & \text{for male} \end{cases}, \quad (8)$$

where e_f and g_f and e_m and g_m are parameter sets for females and males, respectively. In this method, two regressions are sequentially applied; for each size bin, only one intermolt period is roughly estimated and passed from the first regression to the next.

Molting increment is expressed as a linear function that links pre- and postmolt lengths in the double regression model (Ehrhardt 2008):

$$CL_i^* = \begin{cases} h_f CL_i + o_f & \text{for female} \\ h_m CL_i + o_m & \text{for male} \end{cases}, \quad (9)$$

where h_f and o_f and h_m and o_m are parameter sets for females and males, respectively. To eliminate the effect of multiple molts, the records with days-free longer than the corresponding estimated intermolt period are excluded when modeling molting increment.

As with to the likelihood model, bootstrapping has been adopted to estimate parameter uncertainty of both the generalized regression model and the double regression model.

Simulations and comparisons.—Individual-based models (IBMs) are developed to transform deterministic analytic results to sex-specific, sized-based, growth transition matrices using season as a time step. The individual-based models, as described by their names, take the variation of individuals into account (Zhang et al. 2011). The recruitment process is mimicked in the IBMs by adding the growth process that a group of “pseudo” lobsters may encounter in the field. Each “pseudo recruit” represents a number of real recruit individuals, an approach that has been proven to be a simple but efficient solution in modeling the dynamics of large population on an individual basis (Scheffer et al. 1995). To match the analytical models, the temporal resolution of the IBMs is set at a day. Every day, five “pseudo” lobster recruits that are smaller than 46 mm CL enter into the IBM; 46 mm CL is the size at which 1% of female lobsters start to mature (SEDAR 2010). The largest size bin is set as a plus-size bin that includes all lobsters larger than 146 mm CL, as very few lobsters survive to attain that size. The sex, tagging length, and other characteristics (e.g., tagging zone) of the recruits are assigned according to distributions observed from the mark-recapture survey.

We adopted the probabilistic approach in the stochastic simulation. Not only variations, but also correlations of model parameter estimates were used to generate the random sets of growth model parameters for the IBMs. Those parameters, such as molting probability, intermolt period, and the molting increment, were subsequently used to determine the intermediate parameters for each individual “pseudo” lobster. For example, for a lognormal distribution (e.g., the molting increment), random variations were multiplied to the mean value to generate the “customized” parameters for each of the five “pseudo” lobster individuals in every molt. For a probabilistic proportional parameter (e.g., the molting probability in each day), the average values that an individual lobster fell into the group i , p_i , followed a multinomial distribution, and $\sum p_i = 1$. To add variation for each individual lobster, a randomly drawn value, p' , was compared with the cumulative average molting probability in each size bin. If p' was between $\sum_{i=1}^{k-1} p_i$ and $\sum_{i=1}^k p_i$, $1 \leq k \leq n$ (where n is the total number of groups, and $\sum_{i=1}^0 p_i$ is assumed to be 0), the lobster individual would be assigned into group k .

The individual-based models were simulated day after day for 30 years to allow a large number of individuals to reach the largest-size bin. Therefore, all size bins of the growth transition matrices are covered. For each “pseudo” lobster individual, the information related to growth can be recorded every day. For easy comparison, only

seasonal growth information was summarized in the IBM results. The output results of IBMs use the form of 20×20 matrices. Each element in the matrix represents the probability that an individual lobster molts from one 5-mm size bin to the same size bin or another bin. Each individual-based model is simulated 100 times for each fitted statistical growth model to estimate the mean and SD of the growth transition matrices.

Frobenius Norm, also called the Euclidean Norm, is used to calculate the similarity between two matrices (Bhatia 2013):

$$\|\mathbf{G} - \mathbf{M}\|_K = \sqrt{\sum_{i=1}^K \sum_{j=1}^K (g_{ij} - m_{ij})^2}, \quad (10)$$

where \mathbf{G} is the targeted growth transition matrix (e.g., the mean growth transition matrices or their SDs), K is the order of the square matrix \mathbf{G} , \mathbf{M} is a $K \times K$ benchmark matrix, and g_{ij} and m_{ij} are elements in matrices \mathbf{G} and \mathbf{M} , respectively. A smaller value of the Frobenius Norm indicates a greater similarity of the two matrices. In this study, we set the benchmark matrix as the identity matrix when comparing the mean growth transition matrices and used the 0 matrix as the benchmark matrix when comparing the SDs. Based on the assumption that the lobster would not shrink after molting, all lobster individuals would stay in the same size bin if there was no growth, and the growth transition matrix would be the same as an identity matrix. Similarly, if there was no variation in growth, the SD matrix would be 0. A greater dissimilarity of the mean growth from the identity matrix indicates a faster growth, and a greater dissimilarity of the SD from the 0 matrix indicates a larger growth variation. The Frobenius Norm can also be used to track the segmented growth over size bins. The net growth of size bin p can be expressed as the difference of Frobenius Norms between size bins p and $p - 1$, i.e.:

$$\|\mathbf{G} - \mathbf{M}\|_p - \|\mathbf{G} - \mathbf{M}\|_{p-1}.$$

All analyses and simulations were conducted using R version 3.1.1, and the results are visualized by using R and Tableau version 10.0. Due to the limited processing power of a personal computer, a high performance computational resource was deployed.

RESULTS

Using the likelihood model, both the intermolt period and the logarithm of the growth increment could be estimated as functions of the tagging length. The parameter estimates and the covariance are found in Table 1, and the relative growth is demonstrated in Figures 1 and 2.

The results revealed that the female Caribbean spiny lobsters molted less frequently than the males

(permutation test: $p_{molting}^{sex} < 0.05$). Tagging zone and tagging season also affected the molting probability (permutation tests: $p_{molting}^{zone} < 0.05$ and $p_{molting}^{season} < 0.05$). Individual lobsters tagged in the upper Keys or in winter molted less frequently than those in the lower Keys or in summer. No significant difference was observed in the molting probability either between lobsters inside and outside the bay (permutation test: $p_{molting}^{area} = 0.2334$) or between injured or uninjured lobsters (permutation test: $p_{molting}^{injured} = 0.3038$). Therefore, it is reasonable to use only sex, tagging zone, and tagging season in the generalized regression model as categorical factors. Similarly, the molting increment was significantly different between sexes (permutation test: $p_{inc}^{sex} < 0.05$), seasons (permutation test: $p_{inc}^{season} < 0.05$), and areas (permutation test: $p_{inc}^{area} = 0.0854$), although it could have been affected by the significant difference in the observed days free (permutation tests: $p_{days-free}^{sex} < 0.05$, $p_{days-free}^{season} < 0.05$, $p_{days-free}^{area} < 0.05$). The estimates of parameters for the generalized regression model are listed in Table 1, and the relative SD varied from 3.4% to 46.5%.

Table 1 also includes estimated statistics of model parameters for the double regression model, which are sex-specific, but disregard tagging zone and tagging season. Although the same exponential pattern was used in both the likelihood model and the double regression model to describe intermolt period, significant differences were found in the base parameters between the two models (t -tests: $p^{af,ef} < 0.05$ and $p^{am,em} < 0.05$). However, no significant difference was found in the exponent parameters (t -tests: $p^{bf,gf} = 1$ and $p^{bm,gm} = 0.618$). Parameters estimates of the double regression model had larger SD values than did the likelihood model in modeling the intermolt period.

In addition, strong negative correlations were observed between the intercepts and the parameters relating to CL in all three statistical models (Table 2). Such strong correlations could not be found between intercepts and parameters related to the other variables in the generalized regression model.

The estimates of growth contained within the generalized regression model were greater than those of the other models, while the likelihood model had the slowest growth estimations. All statistical models indicated that male lobsters molt faster than females (Figure 1), although the differences between sexes were not significant for the generalized regression model as they were in the other two models (Figure 1). The largest variations with sex and season can be found in matrices estimated from the generalized regression model, and the matrices from the likelihood model has the lowest variations (Figure 1).

In general, net growth decreased exponentially as size increased, but some increases could be noticed (Figure 2A). For example, from the likelihood model results, obvious boosts are found from size bin 4 to size bin 5 for both males and females (61 to 71 mm CL); from the

TABLE 1. Parameters of statistical models used to estimate the growth of Caribbean spiny lobsters using mark–recapture data. CV (%) = 100·SD/mean; subscripts *f* and *m* indicate female and male, respectively.

Model 1: likelihood model						
Step 1	a_f	b_f	a_m	b_m		
Estimate	28.952	0.0278	23.325	0.0234		
SD	7.844	0.00472	6.28	0.00458		
CV (%)	27.1	17	26.9	19.6		
Step 2	c_f	d_f	c_m	d_m		
Estimate	-0.00408	2.199	-0.00447	2.227		
SD	0.00155	0.113	0.0017	0.124		
CV (%)	38	5.1	38	5.6		
Step 2	φ_f	ψ_f	φ_m	ψ_m		
Estimate	-0.00233	-0.662	0.00283	-0.97		
SD	0.00163	0.123	0.0025	0.187		
CV (%)	70	18	89	-19		
Model 2: generalized regression model						
Step 1	a	b	c	d (upper key)	e (winter)	g (male)
Estimate	1.578	-0.0641	0.0631	-0.31	-1.25	0.543
SD	0.275	0.0039	0.00214	0.086	0.113	0.078
CV (%)	17.4	6	3.4	28	8.8	14.4
Step 2	a'	b'	c'	d' (upper key)	e' (winter)	g' (male)
Estimate	2.285	-0.00965	0.00658	-0.072	-0.244	0.12
SD	0.104	0.0014	0.00067	0.033	0.04	0.031
CV (%)	4.5	14.6	10.2	46.5	16.4	25.8
Model 3: double regression model						
Step 1	e_f	g_f	e_m	g_m		
Estimate	33.48	0.0193	38.2	0.0114		
SD	19.86	0.0133	16.068	0.0069		
CV (%)	59.4	68.9	42.1	60.5		
Step 2	h_f	o_f	h_m	o_m		
Estimate	0.963	10.144	0.949	11.289		
SD	0.0132	1.005	0.0155	1.184		
CV (%)	1.4	9.9	1.6	10.5		

double regression model results, a subtle growth boost was only be observed in male individuals from size bin 6 to size bin 8 (71 to 86 mm CL). Most growth occurred in the first six size bins, and limited growth was observed when CL is larger than 76 mm (Figure 2A). Large growth differences among models are reflected in legal-size

lobsters: the likelihood model will lead to the minimum growth, and the generalized regression model will show the maximum growth, while the double regression model will be in between those other models (Figure 2A). The SD among size bins are stable and similar among the three models, except for young lobsters tagged in summer

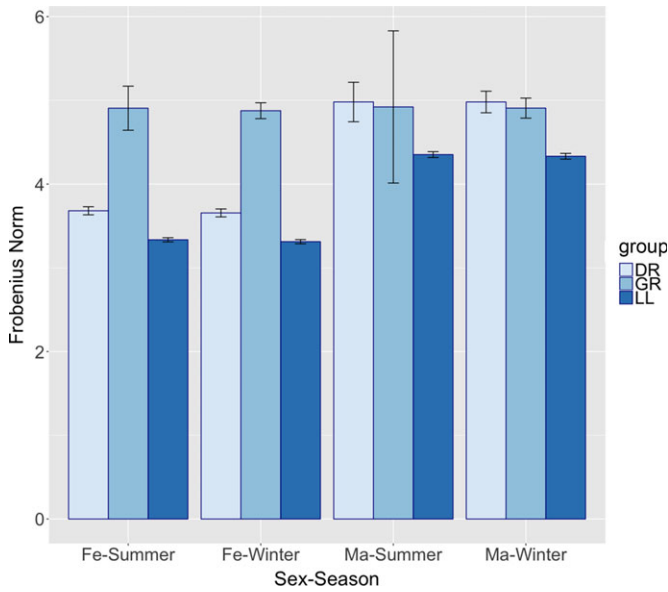


FIGURE 1. The general growth transition matrices (mean \pm SD) for the Caribbean spiny lobster derived from the generalized regression model (GR), the likelihood model (LL), and the double regression model (DR). The y-axis indicates the unitless Frobenius Norms of growth transition matrices; Fe = female, Ma = male.

from the generalized regression model and the male lobsters in size bin 3 from the double regression model (Figure 2B).

Growth transition matrices of the three statistical models can be derived from the IBM, and their means and SDs are provided in Figures S1–S3 available in the Supplement separately online. These matrices can be used directly in future size-structured stock assessment. With the developed growth transition matrices, Frobenius Norm was used to quantify the dissimilarity among models, sexes, and seasons, and also among different size bins. The cumulative trend of net growth for each size bin demonstrates the same conclusion as that found using the Frobenius Norm (Figure S4).

DISCUSSION

For an important fisheries species like Caribbean spiny lobster, a cautionary stock assessment should be employed to ensure that the resource is sustainable for current and future generations. However, there is no effective stock assessment model for the spiny lobster fishery in the southeastern United States (SEDAR 2010). An on-going project has been funded by the Florida Sea Grant to develop a size-structured stock assessment model. For a size-structured model, the growth component is critical, but many stock assessments “fail to document how such matrices are estimated” (Punt et al. 2016). In this study,

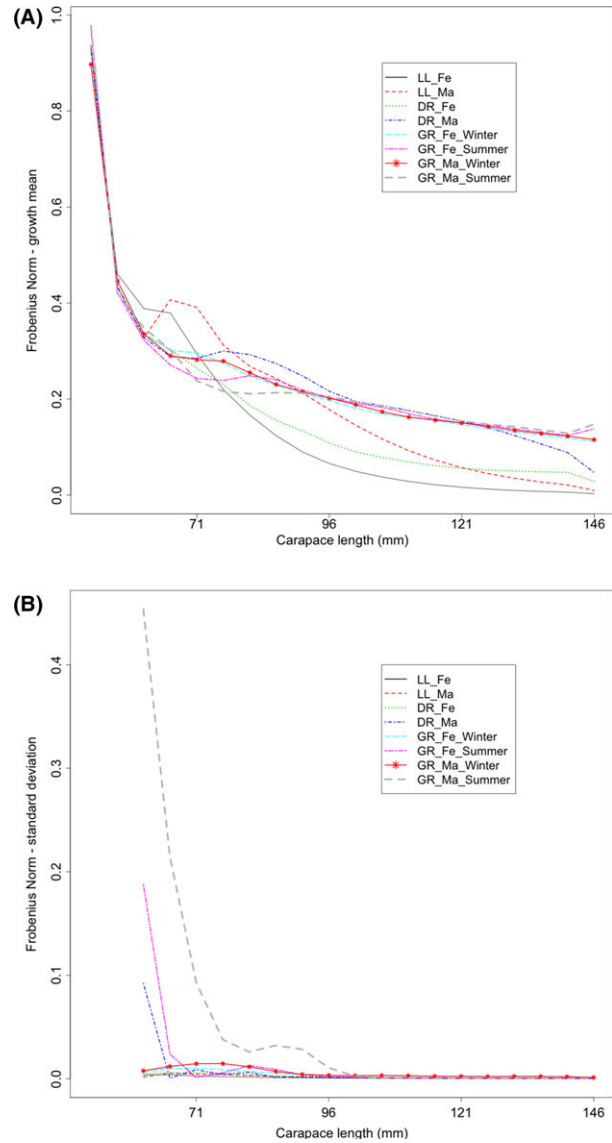


FIGURE 2. (A) Mean and (B) standard deviation of the net growth for the Caribbean spiny lobster over size bins from the generalized regression model (GR), the likelihood model (LL), and the double regression model (DR). Fe = female, Ma = male.

the individual growth of Caribbean spiny lobsters is estimated from a set of mark–recapture data. Mark–recapture data have been frequently used to generate the growth transition matrix. The mark–recapture surveys have been conducted in the Florida Keys for more than 40 years, although without continuous sampling. There was a nearly two-decade gap from 1980 to 1998. A significant difference in molting probability has been found in subgroups before and after the gap ($p_{molting}^{period} < 0.05$). That might be due to the longer days-free periods observed after 1998 ($p_{days-free}^{period} < 0.05$). No such significant difference has been observed in molting increment ($p_{inc}^{period} = 0.2488$). As the mark–recapture data were collected in discrete time

TABLE 2. Correlation coefficients of statistical growth models used to estimate the growth of Caribbean spiny lobsters using mark–recapture data. Subscripts *f* and *m* indicate female and male, respectively.

Model 1: likelihood model					
Step 1	$cor(a_f, b_f)$		$cor(a_m, b_m)$		
Coefficient	-0.886		-0.957		
Step 2	$cor(c_f, d_f)$		$cor(c_m, d_m)$		
Coefficient	-0.989		-0.99		
Step 2	$cor(\phi_f, \psi_f)$		$cor(\phi_m, \psi_m)$		
Coefficient	-0.968		-0.988		
Model 2: generalized regression model					
Step 1	$cor(a, b)$	$cor(a, c)$	$cor(a, d)$	$cor(a, e)$	$cor(a, g)$
Coefficient	-0.945	0.069	-0.149	-0.216	-0.055
Step 2	$cor(a', b')$	$cor(a', c')$	$cor(a', d')$	$cor(a', e')$	$cor(a', g')$
Coefficient	-0.912	0.057	-0.391	-0.079	-0.294
Model 3: double regression model					
Step 1	$cor(e_f, g_f)$		$cor(e_m, g_m)$		
Coefficient	-0.836		-0.954		
Step 2	$cor(h_f, o_f)$		$cor(h_m, o_m)$		
Coefficient	-0.99		-0.99		

periods, 95% of the records were between the years 1975 and 1979, while both the current age-structured stock assessment model and the newly developed size-structured stock assessment model focus more on the period after the year 1990; data for the early and late periods are pooled. The change in molting probability was not taken into account in the analysis, because the 5% of the records after 1998 were not sufficient to afford an accurate and precise analysis. In the future, when longer mark–recapture time series data become available, more growth transition matrices can be developed in a finer temporal scale to track the growth of Caribbean spiny lobster in the southeastern USA.

Multiple statistical analyses have been developed to estimate the growth of the Caribbean spiny lobster (Munro 1974; Hoenig and Restrepo 1989; Muller et al. 1997; Ehrhardt 2008), but few comparisons have been completed to identify the most appropriate one. That is because previous statistical analyses were based on diverse assumptions, constructed by unnested model equations, and fitted by different methods. Thus, it is difficult to compare the results directly. In this study, alternative statistical models were examined using the same data set to review their performances in growth estimation. The methods developed in this study could be further developed to simulate the growth of crustacean species in fluctuating or heterogeneous environmental conditions.

Of the three statistical models compared in our study, the generalized regression model (Muller et al. 1997) revealed the growth differences among the individuals of different sexes and from different seasons and zones. However, the root causes were still concealed. For example,

the model results indicated that the negative effect of the upper Keys tagging zone on lobster growth may not be consistent with reality. The boundary of the upper and lower Keys was determined by diverse geological characteristics: the upper Keys consist of Key Largo limestone covered by sandy-type grains, while the lower Keys consist of Miami limestone covered by the remnants of coral reefs (Hoffmeister and Multer 1968). There has been no direct evidence to prove the relationship between geological characteristics and growth of lobsters. Habitat may be a more reasonable explanation, as seagrass habitats are more energetically profitable (Lipcius et al. 1998) and more preferable for the growth of juvenile lobsters than vegetated habitats (Behringer et al. 2009; Bertelsen et al. 2010). However, if that was the case, the individual lobsters tagged in the upper Keys should be relatively smaller in size and have a higher growth rate, due to the more extensive distributions of seagrass beds (Butler et al. 2005; FLFWC 2016). The inconsistency between the model and reality could result from the significantly different lengths of days-free periods ($P_{days-free}^{area} < 0.05$): Lobsters tagged in the upper Keys have 28.75 days-free on average, which is much longer than the 16.94 mean days-free observed in the lower Keys. A further explanation is that shelters for larger juvenile and adult lobsters are more available in coral reefs (Bertelsen et al. 2010). Higher predation risk in the upper Keys requires longer observation time to get an equivalent sample size as that of the lower Keys. Therefore, we believe the negative effect of the upper Keys in the generalized regression model is related to the effect caused by days-free. Similarly, the significant differences observed between tagging seasons could be attributed to

fluctuating water temperature and/or the varying nutrition and light levels (Travis 1954; Passano 1960) but might be misinterpreted due to the short observation period. Recaptured lobsters with more than 120 days-free were excluded from the training data set, although those only make up 2.5% of the entire tagged population. The generalized regression model will result in large bias in the IBM simulation when the “pseudo” lobsters have longer simulated days-free.

In summary, the generalized regression model adopted flexible link functions that related the linear model of the explanatory variables to the response variable, and the error distributions can be other than natural distributions (McCullagh and Nelder 1989). However, a fundamental assumption of regression is the independence among predictor variables. Interactions among explanatory variables should be carefully considered to avoid bias and minimize errors.

The growth transition matrices derived from the double regression model have smaller SDs than the generalized regression model. However, that does not mean the double regression model has more precise estimations. The smaller variations result from the exclusion of individual variations within size bins (Restrepo and Hoenig 1988), thus dramatically reducing the degrees of freedom provided by the mark–recapture data. Another defect of the double regression model is that the mark–recapture data lack sufficient observations for smaller and larger size bins to estimate a robust median intermolt period (Figure S5). Accordingly, process errors relating to model parameters are amplified.

Unlike the study of Ehrhardt (2008), which integrated experimental data from Sweat (1968) for lobsters from smaller size bins, this study only focused on mark–recapture observations with the purpose of better reflecting growth in natural populations (Sandercock 2006). Plus, integrating experimental data cannot improve the double regression model due to the potential bias and systematic error. Growth experiments for the Caribbean spiny lobster under specified environmental conditions, like water temperature and light, may be relatively easy to imitate artificially, but the spatial–temporal dynamics are always ignored. Moreover, it is impossible to reconstruct diverse habitats within limited laboratory space.

Using inaccurate growth estimations in lobster stock assessment could lead to severe consequences for fisheries management, such as overfishing and stock collapse (Fu and Fanning 2004; Sterner 2007). Most of the differences among the three statistical models were found for the lobsters of sizes larger than 71 mm CL. The likelihood model generated the most conservative growth transition matrices. However, in the likelihood model, the accuracy of the estimated growth parameters is sensitive to the weights assigned to records that fall in each category. Hoenig and

Restrepo (1989) did not include the long days-free, no-molt records, which is equivalent to assuming a minimum penalty weight, e^0 , for likelihood in category 4. A potential effect of this oversight could be underestimation of the intermolt period, where all records in category 4 are misclassified into category 3. An opposite extreme is to assume a large penalty weight, e.g., $e^{-10,000}$. Under that assumption, it is nearly impossible for any mark–recapture records to fall into category 4, and the intermolt period will be overestimated. In this study, we modified the method used in Hoenig and Restrepo (1989) and used a relatively mild penalty weight, e^{-20} , in the likelihood model. This weight was set based on a rough estimation of the average likelihood for each record, which is around 0.8 when the minimum penalty weights in category 4 were assumed. The weight setting also considered the much smaller sample size of the long days-free, no-molt records; only 1% of the records had more than 170 days-free, 15% of which had no increase in lobster size. Therefore, each record that falls into category 4 was amplified 100 times, which makes $(0.8)^{100} = e^{-20}$. In the future, the setting of penalty weights will be refined after discussions with stock assessment scientists.

Growth transition matrices have been commonly used in integrated size-structured stock assessment models (Punt et al. 2013). However, most of the growth processes in fisheries stock assessment reported only the means but ignored the variations (Maunder and Piner 2015). One of the objectives of our study is to account for this missing component for the Caribbean spiny lobster stock assessment. Bootstrapping resampling methods are used to estimate the uncertainty of growth parameters, and then the simulation method is applied to merge multiple probability distributions of correlated parameters into matrices. In the bootstrapping, the ratio between every bootstrap and parent sample sizes is set as 1:1, and the resampling size was determined to be 10,000 because the mean and variation of parameter estimates became consistently stable after 10,000 resamplings in all three statistical models (Figures S6–S8). When the three statistical models are compared, growth estimated from the likelihood model has the smallest variation. The robustness makes the growth transition matrices derived from the likelihood model more suitable for the future Caribbean spiny lobster stock assessment in reducing the uncertainty of the assessment results (FAO 1996; Restrepo and Powers 1999).

Restrepo and Hoenig (1988) proposed the effect of tag loss and mortality on estimated growth. In the comparison of the three statistical models, the molting probability of the generalized regression model will be directly affected by tag loss and mortality, while the intermolt period of the double regression model will be indirectly affected. The likelihood model will be the least-affected model under given tag loss and mortality due to the employment of the maximum likelihood estimation.

One imperfection of the current mark–recapture data is that the samples are collected in different zones without temporal overlap, which should be avoided if any new mark–recapture survey program is designed to provide updated growth information for the Caribbean spiny lobster in the Florida Keys. A long observation period needs to be incorporated with the purpose of providing sufficient information about the intermolt period for the lobsters that take longer than one season to molt. Also, balanced samples should be collected from both the heavily harvest areas and no-take zones (SEDER 2010). Federal fishery regulations forbid Caribbean spiny lobster harvest in the Dry Tortugas National Park and Florida Keys National Marine Sanctuary (U.S. Office of the Federal Register 1997). Compared with no-take zones, fishing areas would have fewer large individuals available for harvest. Therefore, the average growth will be overestimated in heavily harvested areas and may be underestimated in no-take zones.

In conclusion, this study improved an analytical growth model for the Caribbean spiny lobster and was the first time that all previous analytical growth models for Caribbean spiny lobster had been examined with the full mark–recapture data set. Growth transition matrices were developed for future stock assessment models, and the uncertainty was also estimated. By using the Frobenius Norm and the simulation method, unnested analytical models developed on various assumptions can be compared.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.