A new approach to compare and integrate mark-recapture and length-frequency analysis - with a case study on body growth and mortality of giant land crabs (*Cardisoma guanhumi*)

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Abstract

Tagging and length-frequency analysis (LFA) are common methods to study body growth and mortality in populations of fish and invertebrates, but little has been done to assess and compare the inherent uncertainty of these methods. This study applies a new bootstrap-based approach, within the fishboot R package, to a case study of semi-terrestrial crabs (*Cardisoma guanhumi*). Crabs were sampled at upper mangrove fringes of Itamaracá Island over 12 months, from April 2015. A total of 1,078 individuals were captured and measured. Among these, 291 individuals were marked with PIT (passive integrated transponder) tags. 130 size increments were obtained. Carapace widths varied from 20.9 to 70.0 mm (mean: 43.4 mm). Tagging and LFA produced similar median parameter estimates, but tagging produced significantly (p < 0.0001) narrower 95% CIs. Estimates for K from tagging were 3 times more precise than from LFA, estimates for L∞ were 2.2 times more precise. Both methods indicate very slow growth and L∞ far above Lmax. Tagging-based estimates were K = 0.12 y⁻¹ (95% CI: 0.024 to 0.26 y⁻¹), L∞ = 118 mm (95% CI: 81 to 363 mm), \( \Phi' = 1.23 \log_{10}(\text{cm y}^{-1}) \) (95% CI: 0.86 to 1.36 \( \log_{10}(\text{cm y}^{-1}) \)). Seasonality in growth was significant (p = 0.006, 95% CI for C: 0.15 to 0.93, median: C = 0.56). Age of captured individuals was 1.5 years (20.9 mm) to 7.0 years (70.0 mm). A two-step non-parametric bootstrap was used to assess Z and to investigate the log-linear relationship (slope = 1) between Z and input growth parameters, with implications for previous meta-analyses. We confirmed the usefulness and robustness of \( \Phi' \), and its close relation to Z. While estimates of K and Linf were very imprecise, they formed well-structured pairs along a narrow \( \Phi' \) isopleth, leading to a high precision for \( \Phi' \). Total mortality was Z = 2.18 y⁻¹ (95% CI = 1.7 to 4.5 y⁻¹). Recruitment was
continuous, with an increase in the dry season. Slow growth and a very high Z/K ratio for this population confirm the need for protective measures. Implications for length-based studies of growth and mortality are discussed.

Key words: mangroves; semi-terrestrial crabs; growth; mortality; tagging; new methods

1. Introduction

Knowledge of growth and mortality and their inherent uncertainty is fundamental for the management of exploited populations. Length-frequency analysis (LFA) and tagging and are common methods to study populations of fish and invertebrates, but little has been done to assess and compare the inherent uncertainty of these methods.

Tagging is generally considered to be very precise and accurate (Schmalenbach et al., 2011; Tang et al., 2014), since for each recaptured individual, its most recent size increment (dL/dt) is determined with great precision and accuracy. However, variability in growth will always lead to a certain level of uncertainty regarding the estimation of average growth parameters of the whole population (Hufnagl et al., 2012; Schwamborn et al., 2018b). This uncertainty may be substantial, given the often low N of recaptured individuals. Tagging has several additional advantages and by-products, such as the determination of population size and the study of migrations and site fidelity (Moraes-Costa and Schwamborn, 2018). However, tagging
campaigns are often very costly and generally require a huge effort (Schmalenbach et al., 2011). Also, tagging may be difficult, or even impossible, for widely spread, small organisms, such as small-sized shrimp, where LFA is the only available approach (Hufnagl et al., 2011).

On the other hand, LFA requires only the regular capture and measurement of organisms (not necessarily purchase or sacrifice). This is probably the main reason why LFA remains hugely popular for stock assessment and population studies, since its first application in the late 19th century (Petersen, 1891). In most traditional methods for LFA, only one-point estimates are given for growth parameters, without any measures of uncertainty. More seriously, many common length-based methods, such as the Powell-Wetherall plot (Wetherall, 1986, Pauly, 1986), may be severely biased (Hufnagl et al., 2012, Schwamborn, 2018), which indicates the need for new approaches and toolboxes.

It is well known that when fitting the von Bertalanffy growth function (VBGF, von Bertalanffy, 1934, 1938) to any given data set, a larger asymptotic size $L_\infty$ will lead to a reduced growth coefficient $K$ and vice-versa (Shepherd et al., 1987; Kleiber and Pauly 1991; Pauly and Greenberg, 2013; Schwamborn et al., 2018b), making the estimation of uncertainty in $L_\infty$ and $K$ estimates, each for itself, very complex, or even impossible. The projection of a grid of regularly spaced $K$ and $L_\infty$ values, together with a resulting “quality of fit” estimator ($R_n$), in the form of 3D plots or heatmaps (i.e., the “response surface”, Brey et al., 1988; Isaac, 1990; Kleiber and Pauly 1991; Gayanilo et al., 1995), for a given data set, will ideally produce a bent ellipse or “banana-shaped plateau” (Pauly and Greenberg, 2013). The popular “Response Surface Analysis” (RSA), using a coarse heatmap, allows for a simultaneous search for an “optimum”
combination of K and $L_\infty$ (Gayanilo et al., 1995), but RSA cannot provide any confidence intervals or bi-dimensional confidence contour envelopes. This can only be accomplished by Bayesian approaches (Tang et al., 2014), or by non-parametric bootstrapping (Schwamborn et al., 2018b).

Here, we apply a new bootstrap-based approach (fishboot R package) to a case study of "giant", or "blue", land crabs *Cardisoma guanhumi* (Latreille, 1825). This species occurs from Florida to southern Brazil on the upper fringes of mangroves and adjacent lowlands, where it is generally the largest and most conspicuous brachyuran crab species in these coastal ecosystems (Tavares, 2003). In Florida and in the Caribbean, local $L_{\text{max}}$ may often reach more than 100 mm carapace width (Forsee and Albrecht, 2012). These semi-terrestrial crabs are considered an important food source in some countries, e.g., in Venezuela (Carmona-Suárez, 2011) and in Brazil (Silva et al., 2014). In northeastern Brazil, *C. guanhumi* is a high-value resource and a very important source of income for the poorest fishermen, also being an intrinsic part of local culture (Schwamborn and Santos, 2009; Firmo et al., 2012; Shinozaki-Mendes, et al., 2013). Additionally to commercial capture by fishermen, these land crabs suffer a high predation pressure from numerous small mammals, such as crab-eating raccoons (Moraes-Costa and Schwamborn, 2018). *C. guanhumi* is considered a critically endangered species in Brazil, the main threats being unsustainable harvesting and the destruction of mangroves and adjacent salt flats, e.g., for urbanization and shrimp farms.

Acknowledging its endangered status, two Brazilian federal laws have been passed recently (in 2014 and in 2016), prohibiting the capture, transportation, storage, management, processing and
marketing of this species. Previous protection measures were the capture of males only, a minimum legal size (60 mm carapace width) and a seasonal closure from December to March. These measures, were, however, poorly respected and proved ineffective, leading to severe overharvesting. Thus, *C. guanhumi* has recently been listed as “critically endangered”. This led to a complete prohibition of the capture of this species in Brazil, pushing thousands of crab harvesters into illegality, and leading to an enduring controversy among stakeholders and the scientific community. In spite of its huge socio-economic importance and its endangered status, little is known about growth and mortality of this species (Botelho et al., 2001; Silva et al., 2014; Moraes-Costa and Schwamborn, 2016).

The objectives of this study were to assess growth and mortality of severely threatened land crabs (*Cardisoma guanhumi*), including its inherent uncertainty, and to test and present a new bootstrap-based approach for integrated LFA and tagging analyses of growth and mortality.

2. Materials and Methods

2.1. Study area

The study area is a well-preserved mangrove patch located inside the National Center for Research and Conservation of Aquatic Mammals of the Brazilian ICMBio agency (CMA /
ICMBio), at Itamaracá Island, Pernambuco State, Brazil (07° 48’ 36” S, 034° 50’ 26” W at 07° 48’ 31” S, 034° 50’ 15” W).

The vegetation inside the study area is dominated by the mangroves *Rhizophora mangle* and *Conocarpus erectus*. Four sampling areas (A, B, C and D) were defined at the upper fringe of the mangrove, where *Cardisoma guanhumi* burrows were observed (Moraes-Costa and Schwamborn, 2018). Additionally to the mangrove tree species *R. mangle* and *C. erectus*, typical beach vegetation also occurred at the sampling sites, such as *Terminalia catappa* and *Syzygium cumini*, forming a line of dense shrubs at the upper margin of the mangrove.

According to the classification of Köppen (APAC, 2016), the climate of Itamaracá Island, Pernambuco, is of the wet tropical type Ams’ (Manso, 2006). The rainy season in this region reaches from March to August, the peak dry season from November to January. Monthly accumulated rainfall values at Itamaracá during peak rainy season, in June and July 2015, were 234.1 mm and 291.0 mm, respectively. During the peak dry season months, rainfall in Itamaracá was zero in November 2015, 88.5 mm in December 2015 and 65.2 mm in January 2016 (APAC, 2016). The locally measured differences in air temperature, between the highest monthly average (27.5 °C, January 2016) and the lowest monthly average (24.3 °C, July 2015), result in a seasonal temperature amplitude of 3.2° C.

**2.2. Sampling Strategy**

Monthly sampling was conducted during one year, from February 2015 to March 2016, along the upper fringe of the CMA mangrove. Cylindrical traps, identical to those used by artisanal
fishermen, were built with plastic bottles and cans. Inside each trap, a pineapple fragment was used as bait, as done in regular artisanal harvesting. A total of 70 artisanal traps were built for this study. Each trap was positioned at the entrance of a burrow for forty-eight hours and evaluated every two hours. The individuals captured in each sector were distributed into twelve plastic boxes of 70 x 30 cm and allocated by sector and size group (maximum: 15 individuals per box, the bottom of the boxes covered with humid mangrove branches as to avoid stress and aggression), prior to measuring and tagging. All individuals were measured (carapace width, length and height) weighed, sexed, and released. Sex ratio (ratio of captured males: females) was tested for a significant difference from equality by a simple Chi-square test (Zar, 1996).

2.3. Tagging with PITs

Of the 1,078 individuals captured, 291 individuals (153 males and 138 females), or 27%, were tagged with passive integrated transponder tags (PIT, Nanotransponder tags, Trovan, model ID 100 A, dimensions: 1.25 mm x 7.0 mm). The tagged individuals had a carapace width of 24.4 to 59.5 mm (standard deviation: 7.4 mm).

PITs were always inserted into the ventral part of the carapace through the base of the fourth pereiopod, by injection with a specific syringe-type applicator. Each PIT has a unique numbering, which can only be obtained through a specific reader (Vantro Systems, model GR250).
To assess tag loss, a heat mark (quick branding with a soldering iron) was made on the upper part of the carapace (Diele and Koch 2010), which served as control at the time of recapture, indicating a tagged individual.

2.4. *Sex-specific growth and mortality*

Growth in size (carapace width, mm) was described using the von Bertalanffy growth function (VBGF, von Bertalanffy, 1934, 1938), based on analyses of length-frequency distributions (LFDs) and on mark-recapture with PITs. The shape of the VBGF is mainly determined by two parameters: the growth constant \( K \) and the asymptotic length \( L_\infty \). The growth performance index \( \Phi' \) (“Phi-prime”, Pauly and Munro 1984) was used to obtain a proxy that integrates \( L_\infty \) and \( K \), where \( \Phi' = \log_{10}(K(y^{-1})) + 2 \log_{10}(L_\infty(cm)) \).

Total mortality \( Z \) was estimated using the length-converted catch curve (LCCC) method (Baranov, 1918, Ricker, 1975, Pauly, 1983, 1984a, 1984b). Differences between males and females regarding all relevant population parameters (mean size, median size, mean growth increments, \( K \), \( L_\infty \), \( Z \), etc.) were tested at \( p_{crit} = 0.05 \) using a non-parametric permutation test (function `independence_test` in the R package `coin`, Hothorn et al., 2006).
2.5. **Length-frequency analysis**

All individuals were grouped into size class intervals of 2 mm as to obtain monthly length-frequency distributions (LFDs). Growth parameters $L_\infty$ and $K$ were estimated directly, based on the monthly LFD plots, using the ELEFAN I method (Eletronic LEngth-Frequency ANalysis, Pauly and David, 1981), inserted in the FISAT II (Gayanilo et al. 1996, Gayanilo and Pauly, 1997) and *TropFishR* (Mildenberger et al., 2017) software packages. To detect peaks (i.e., cohorts), ELEFAN I uses a moving average (MA) smoothing function, where the original LFDs (black bars in Fig. 1a) are transformed as differences between the smoothed curve and the original, resulting in a sequence of positive (peaks) and negative (troughs) values (black and white bars in Fig. 1b). The moving average span (MA = 7) for ELEFAN I was chosen based on the rule of thumb suggested by Taylor and Mildenberger (2017), where MA should be approximately equal to the number of bins spanning the youngest cohorts.

Additionally, the Bhattacharya (1967) method, also a part of the FISAT II package, was used to determine the peaks of the cohorts (green dots in Fig. 1a). This common method decomposes the frequency distributions into normally distributed cohorts with precise, unique peaks. A VBGF curve can be constructed by manually connecting these Bhattacharya peaks (Sparre and Venema, 1998).
2.6. The Powell-Wetherall method

A simple, straightforward LFA approach is generally recommended to fit a VBGF curve to LFD data, which consists in quickly determining $L_\infty$ and then conducting a detailed search for an optimum value of $K$, using a fixed value for $L_\infty$ (Gayanilo et al., 1995, 2005; Mildenberger, 2017). The first step is to obtain a single estimate of $L_\infty$, either by using the Powell-Wetherall method (P-W method, Wetherall, 1986; Pauly, 1986; Schwamborn, 2018), or directly based on the largest organism in the sample (“Lmax approach” or maximum-length approach, Mathews and Samuel, 1990; Schmalenbach, 2011; Schwamborn, 2018). Here, the P-W plot method, also called the "modified Wetherall method" (Wetherall, 1986, Pauly, 1986) was used as an additional and independent method to estimate $L_\infty$ and the mortality/growth (i.e., $Z / K$) ratio. The P-W method, originally proposed by Wetherall (1986), and modified by Pauly (1986), is based on partitioning a catch curve in consecutive cutoff lengths. The parameters (intercept and slope) of a linear regression are used to calculate the $Z / K$ ratio and $L_\infty$ (Pauly, 1986). Different versions of the original and modified P-W methods were tested with the C. guanhumi LFD data, using FISAT II (Gayanilo et al., 1995, 2005), “ELEFAN in R” (Pauly and Greenberg, 2013) and “TropFishR“ (Mildenberger et al., 2017).

Two widely recommended (Sparre and Venema 1998) and commonly used approaches (“traditional LFA approaches”) were used for determining the growth coefficient $K$: ELEFAN I (Pauly and David 1981) with K-Scan (scanning a series of K values, using a fixed $L_\infty$ value, previously obtained from the P-W method, Gayanilo et al., 1995, Moraes-Costa and
Schwamborn, 2016), and Response Surface Analysis (RSA, Gayanilo et al., 1995). These methods were used by applying the widely used FISAT II software (Gayanilo et al., 2005) and, for comparison, the R package TropFishR (Mildenberger et al., 2017). In TropFishR, the genetic search algorithm ELEFAN_GA (Mildenberger et al., 2017) was used to fit growth models to the monthly LFDs, using precision-optimized search settings (e.g., maxiter = 100), and searching within a nearly unconstrained (i.e., extremely wide) search space (e.g., $L_\infty$ from 0.5 * $L_{max}$ to 15 * $L_{max}$, K from 0.01 to 1, and C from 0 to 1). Only one single curve fit attempt and one fixed seed value were used for ELEFAN_GA. Then, multiple, automatically repeated fit attempts, using the same, original LFDs, using only different seed values (i.e., conducting a partial bootstrap sensu Schwamborn et al., 2018b) were conducted using the function ELEFAN_GA_boot (Schwamborn et al., 2018a).

2.7. Tagging-based analyses

Body growth was also investigated by analyzing data obtained from mark-recapture. The input data were individual size increments, that is, two sets of paired variables: time lags (dt) and size differences (dL), for each recapture event. Increments in carapace width (dL/dt, in mm year$^{-1}$) were inserted into the fishmethods R package (Nelson, 2018). The grotag function (Kienzle and Nelson, 2018) was then applied to these increments, using the nonlinear adjustment method proposed by Francis (1988). The individual growth increments and the growth parameters K and $L_\infty$ obtained with grotag were then used as inputs to plot these increments on a VBGF curve (Fig. 2) using the growthTraject function (Hoenig, 2018) within the fishmethods package (Nelson,
2018). For comparison, we also tested the use of the Munro and Gulland Holt methods, using the 
growth_tagging function within the TropFishR package (Mildenberger et al., 2017).

2.8. Seasonal growth

Additionally to the common VBGF, the seasonally oscillating von Bertalanffy growth function
was also used in this study (soVBGF, Ursin, 1963a, 1963b; Pitcher and MacDonald, 1973; Pauly
and Gaschütz 1979; Francis, 1988; Somers, 1988). The soVBGF has two additional parameters:
the seasonal amplitude “C” (Pauly and Gaschütz, 1979) and a location parameter (e.g., winter
point, WP). The seasonal amplitude “u” in Francis (1988) given by the function grotag in the R
package fishmethods is identical to the seasonal amplitude ”C” in Pauly and Gaschütz (1979) and
in ELEFAN I (Pauly and David 1981). If \( u = 0 \), there is no seasonal variation, if \( u = 1 \), growth is
zero in winter. The winter point “WP” of minimum growth in ELEFAN I is the opposite of “w”
(date of maximum growth, i.e., “summer point”) estimated from tagging data using grotag
(Francis, 1988). WP was obtained from grotag outputs by \( WP = w + 0.5 \).

Two statistical procedures were used to verify whether there is a significant seasonality in
growth. First, general additive models (GAM, Hastie and Tibshirani, 1990) were applied to
monthly growth time series obtained from mark-recapture. GAM models were built for raw
growth increments (dl/dt) and for the residuals of the non-season VBG curve, using the gam
package (Hastie, 2018) in R at \( p_{crit} = 0.05 \).
Also, a Mann-Whitney U-test ($p_{\text{crit}} = 0.05$) was conducted to test for significant differences of the median increments ($dL / dt$) between rainy and dry season (Zar, 1996). This test was based only on increments with less than 65 days of duration, that is, only increments with one and two months intervals were used for this seasonality analysis. Rainy season growth: increments ($dL / dt$) in carapace width (mm year$^{-1}$) of individuals recaptured from July to October 2015 (marked May to September 2015. Rainy season growth: increases ($dL / dt$) of carapace width (mm / year) of individuals recaptured in May 2015, and recaptured from December 2015 to March 2016 (marked April 2015 and marked October 2015 to February 2016).

2.9. Integration of length-based and tagging-based methods into a seasonal growth curve

Once a set of reliable estimates of $K$ and $L_\infty$ had been obtained through tagging-based methods (fishmethods package), a new evaluation of the LFDs was made using a multi-step approach applying different ELEFAN I-based routines, to verify whether the growth curve obtained by tagging can be applied to the monthly LFDs, and to obtain final best fit estimates for growth parameters, by fine tuning and repeated fitting.

In this final step, growth, mortality (length-converted catch curve LCC, Pauly, D., 1983, 1984a, 1984b) and recruitment (Pauly, 1982) were assessed using FISAT II and TropFishR (Gayanilo et al., 2005; Mildenberger, 2017). Recruitment patterns were also assessed by plotting the monthly abundance of small individuals (CW < 30 mm).
A new attempt was made to fit the VBGF growth curve to the monthly LFDs data, based on the K and $L_\infty$ estimates obtained with the fishmethods package, using ELEFAN I (applying the function ELEFAN_GA in the TropFishR package) to estimate only the SS (starting sample) and SL (starting length), with fixed K and $L_\infty$, as to obtain a single preliminary fit of the non-seasonal and seasonal VBGF curves to the monthly LFD data. Finally, the function ELEFAN_GA_boot in the fishboot package (Schwamborn et al., 2018a) was used to determine the final best fit parameters of the soVBGF curve (best fit values for K, $L_\infty$, C and ts) based on 1,000 repeated independent fitting attempts.

2.10. Uncertainty in growth

Confidence intervals (CIs) for growth parameters were obtained by bootstrapping two datasets: mark-recapture growth increments and monthly LFDs (Efron, 1979, 1987; Schwamborn et al., 2018b). When bootstrapping tagging-based growth estimates, in each run, a random sample (of same size as the original data) was taken from the size increment data, with replacement. The grotag function (Kienzle and Nelson, 2018) within the fishmethods package was then applied to these resampled increments, based on the nonlinear adjustment method proposed by Francis (1988), as to obtain unique values of K, $L_\infty$ and $\Phi'$ for each bootstrap run. Simple random sampling was repeatedly applied with replacement, using the standard sample function in R (at least 1,000 runs). This bootstrap routine for growth increments was built into the function grotag_boot within the new fishboot package (Schwamborn et al., 2018a). 95% CIs were then obtained from percentiles of the posterior distributions for K, $L_\infty$ and $\Phi'$. Bivariate confidence
contour envelopes (Fig. 4) were drawn using the \textit{LinfK\_scatterhist} function of the \textit{fishboot} package (Schwamborn et al., 2018a), based on 1,000 successful bootstrap runs.

Uncertainty in growth was also assessed for growth parameters K, \(L_\infty\), C and ts estimated by LFA. For this purpose, 95% CIs were calculated by using the \textit{ELEFAN\_GA\_boot} function in the \textit{fishboot} R package (Schwamborn et al., 2018a), which is a bootstrapped version of the \textit{ELEFAN\_GA} curve fitting function in \textit{TropFishR} (Mildenberger et al., 2017). The function \textit{ELEFAN\_GA\_boot} was used with 1,000 bootstrap runs applying the following precision-optimized parameters: \(MA = 7\), \texttt{seasonalised = TRUE}, \(maxiter = 100\), \(run = 40\), \texttt{addl.sqrt = FALSE}, \texttt{parallel = TRUE}, \(\texttt{low\_par = NULL}\), \texttt{popsizesize = 50}, \texttt{pmutation = 0.2}, \texttt{low\_par = list (\(L_\infty\) = 35 mm, K = 0.01, t\_anchor = 0, C = 0, ts = 0)}, \texttt{up\_par = list (\(L_\infty\) = 1050 mm, K = 1, t\_anchor = 1, C = 1, ts = 1)}, following the recommendations given in Taylor and Mildenberger (2017) and in Schwamborn et al. (2018b). For each bootstrap analysis, duration per run (min. \textit{run}^{-1}) was recorded, using a common PC with six-core CPU (AMD FX-6300, 3.5GHz). Bivariate confidence contour envelopes (Fig. 4) were drawn using the function \textit{LinfK\_scatterhist} in the \textit{fishboot} package (Schwamborn et al., 2018a, 2018b, 2019), based on 1,000 successful bootstrap runs.

2.11. Comparing the precision of methods

To test for significant differences in the precision of methods (\textit{e.g.}, tagging vs LFA), a interquantile range test (Schwamborn, 2019), \textit{i.e.}, a non-parametric test for the comparison of inter-quantile ranges of bootstrap posteriors, was conducted, as described in Schwamborn et al.
(2018b) and in Schwamborn (2019). The interquantile range test was used as implemented in the R function `interquant_r.test` within the `fishboot` package (Schwamborn et al., 2018a), at $p_{crit} = 0.05$.

2.12. *Simulations to investigate relationships between growth and mortality parameters*

Simulations were conducted to investigate possible linear relationships between input growth parameters and output mortality estimates. For this purpose, pairs of independent simulated data (1,000 pairs of $K$ and $L_\infty$ values) were used as inputs to calculate $Z$ by the LCCC method, applied to the real *C. guanhumi* catch curve obtained from the Itamaracá mangroves. Two independent data sets with 1,000 random uniform numbers ($L_\infty$ from 70 to 130 mm and $K$ from 0.06 to 0.8 $y^{-1}$) were used as input, and applied to the *C. guanhumi* catch curve, using the LCCC method as described above. Simple linear models of $K$ vs $Z$, $L_\infty$ vs $Z$, and $\Phi$’s vs $Z$ were used to investigate potential relationships between input growth parameters and output mortality (blue dots and green dotted line in Fig. 5).

2.13. *Two-step bootstrap to assess uncertainty in mortality estimates*

A two-step-bootstrap approach was used to assess uncertainty in mortality estimates. Step one was to bootstrap the `grotag` function to obtain posterior distributions for $K$ and $L_\infty$ (see above). Step two was to apply these $K$ and $L_\infty$ values to build LCCC plots and obtain a large number of $Z$ values, i.e., a posterior distribution for $Z$. The posterior distribution for the $Z$ central estimate
considers only the uncertainty in the procedures leading to the LCCC, while the full, merged posterior distribution (posterior distributions for the Z central estimate, upper and lower 95% CI estimates for Z from the LCCC linear regression model) considers the uncertainty in both steps (pre-LCCC steps and LCCC linear regression model).

Z/K ratios were calculated based on posterior distributions of K from tagging and posteriors of Z from two-step-bootstrap with LCCC. These two posterior distributions were combined with a simple Monte Carlo approach, where a sample (n = 1) was taken randomly from each of the two posterior distributions, to calculate a set of unique Z/K ratios. This was done repeatedly (1,000 runs) and Z/K ratios were saved for posterior analysis. This posterior distribution of 1,000 Z/K values was used to calculate CIs for Z/K.

In this study, all 95% CIs were calculated based on the 0.025 and 0.975 quantiles of posterior distributions, using the quantile function in standard R (R Development Core Team 2019).
3. Results

3.1. Length-frequency analysis

In this study, a total of 1,078 individuals of *C. guanhumi* were caught and measured. Carapace width (CW) ranged from 20.9 mm to 70.0 mm, with a mean of 43.4 mm (standard deviation: 8.5 mm, median: 44.0 mm). Total weights varied between 4.0 g and 162.0 g, with a mean of 45.8 g (standard deviation: 25.3 g, median: 44.0 g). Sex ratio between 572 males (53%) and 506 females (47%) was significantly different from equality (sex ratio = 1.13: 1, $\chi^2 = 3.93$, p = 0.047). No significant differences in size or weight parameters were detected between sexes (permutation test, p > 0.05). Thus, all LFAs were conducted with pooled (males and females) data. The vast majority (99.2 %) of all captured individuals were adults, with only 14 juveniles.

Multi-modal distributions were observed in all months, with up to seven distinct modes per month (Fig. 1). There was no evident, unique modal progression to be observed in these data, whether using Bhattacharya, Shepherd’s method, ELEFAN I in FISAT II, or the *ELEFAN_GA* function in *TropFishR*. For instance, the Bhattacharya method produced a complex map of multiple modes (green dots in Fig. 1), which can be subjectively connected in numerous ways, offering many different potential growth curves. Shepherd’s method and ELEFAN I also provided several possible solutions (growth curves), with nearly identical goodness of fit (Rn) values.
Standard optimization routines using a P-W plot and subsequent ELEFAN I with K-scan or Response Surface Analysis (RSA) did not produce a single optimum result, neither. When using the FISAT II software (ESM Table 1), the P-W method produced a Z/K ratio of 4.2 and a $L_\infty$ estimate of 75.9 mm (close to the $L_{\text{max}}$ value of 70 mm). When using TropFishR, $L_\infty$ estimates obtained from P-W plots varied from 69.3 to 75.9 mm (depending on subjective point selections). When using the P-W method in TropFishR, 95 % CIs for $L_\infty$ varied from 48.9-89.7 to 30.6-119.2 mm, and Z/K estimates varied from 3.1 to 4.8 (95% CIs for Z/K varied from ZK 3.1-3.2 to 4.7-4.9).

The K-Scan routine in FISAT II yielded three peaks of approximately equal height, with three possible “optimum“ K values: 0.15, 0.21, 0.38 (all had Rn Scores of 0.20 to 0.21). When using the traditional RSA method (within FISAT II and TropFishR), the best VBGF growth model ($L_\infty = 72.5$ mm; $K = 0.38$) had a Rn Score of 0.21, and was similar to one of the ‘optimum’ results obtained by K-Scan. The optimal $L_\infty$ estimate obtained with RSA within FISAT II ($L_\infty = 72.5$ mm) was very close to $L_{\text{max}}$ (70 mm) and to the $L_\infty$ estimate obtained with Powell-Wetherall plot method (75.9 mm) within FISAT II.

The optimization routine ELEFAN_GA within TropFishR, that was used to fit VBGF curves within a nearly unconstrained $L_\infty$ and K search space, produced numerous possible results, too, depending on the initial seed values. The “best fit” varied strongly between subsequent optimization runs, with strongly varying “best fit” estimates, showing the tendency of this
optimization method to become trapped in a different local maximum within the RSA space in each run, even when using very time-consuming and precise optimization settings (e.g., maxiter = 100). Best fit estimates obtained for $L_\infty$ varied between 67.4 and 123.9 mm (mean: 91.3 mm, median: 84.58 mm) and K values between 0.076 and 0.5 $y^{-1}$ (mean: 0.199 $y^{-1}$, median: 0.151 $y^{-1}$). Rn scores varied from 0.201 to 0.294. After 100 subsequent optimization runs (i.e., after 100 runs * 100 iterations = 10,000 iterations), the best non-seasonal VBGF fit parameters obtained with ELEFAN_GA were $L_\infty = 110.6$ mm, $K = 0.094$ $y^{-1}$, $t_{anchor} = 0.741$ a and Rn Score = 0.294, indicating very slow growth, much slower than from traditional methods, and very large $L_\infty$, much larger than from the P-W method and considerably larger than local $L_{\text{max}}$ (70 mm).

3.2. Mark-recapture results

Among the 291 individuals that were successfully tagged with PIT tags (153 males and 138 females), 95 individuals were recaptured at least once. Tagging yielded 130 useful growth increments (dL/dt), where 84 individual increments were obtained from males and 46 from females. No significant differences in growth increments were detected between sexes (permutation test, p > 0.05).

The number of increments (130) is larger than the number of recaptured individuals (95), since several individuals were recaptured more than once. The maximum number of times a single individual was recaptured was five. Sixty-six individuals (69%) were recaptured twice; twenty-
two individuals (23%) were recaptured three times; six individuals (4.6%) were recaptured four times, and one individual (1%) was recaptured five times.

All 130 size increments could be combined into one single VBGF curve using the `grotag` function in `fishmethods` without any adjustments or exclusion of outliers (green line in Fig. 2). Conversely, the `growth_tagging` function within `TropFishR` did not converge towards useful results, producing negative numbers or results at the upper margin of any predefined search space. The optimum growth parameters for all mark-recapture data (males and females) given by using `fishmethods` were $K = 0.145 \text{ y}^{-1}$; $L_\infty = 108.03 \text{ mm}$. Growth parameters were very similar between sexes ($L_\infty^{\text{males}} = 105 \text{ mm}$; $L_\infty^{\text{females}} = 109 \text{ mm}$; $K^{\text{males}} = 0.16 \text{ y}^{-1}$; $K^{\text{females}} = 0.13 \text{ y}^{-1}$). The age of the individuals captured ranged from 1.5 years (20.9 mm) to 7.0 years (70.0 mm). $L_\infty$ obtained from mark-recapture (108 mm) was very similar to the best $L_\infty$ value obtained with `ELEFAN_GA` (110 mm) and considerably larger than values obtained from traditional LFA (P-W plot in FISAT II, $L_\infty^{\text{Powell-Wetherall}} = 75.9 \text{ mm}$). Accordingly, the estimate of $K$ from mark-recapture was much lower than from traditional LFA methods (ESM Table 1), leading to entirely different shapes of the growth curves obtained with these two methods (green line vs dashed red line in Fig. 2).

### 3.3. Seasonal recruitment and growth

Recruitment was continuous throughout the year, with lower recruitment during the rainy season (Fig. 3a). Seasonal variation in growth was well described with a non-linear GAM model (Fig. 3a).
3b), which was significantly different from zero (p = 0.022). Pairwise tests also showed that increments were significantly smaller in the rainy season than in the dry season (p = 0.006, n = 44 increments, Mann-Whitney test). Mean growth in the dry season was 5.1 mm y⁻¹ (st. dev.: 9.8 mm y⁻¹). Conversely, mean growth in the rainy season was negative, with -1.1 mm y⁻¹ (st.dev.: 2.9 mm y⁻¹).

3.4. Fitting a seasonally oscillating growth curve

When applying the seasonally oscillating soVBGF, the best fit also varied strongly between subsequent ELEFAN_GA runs, with strongly varying ‘optimum’ estimates, showing the tendency of this optimization method to become trapped in a different local maximum within the search space in each run (when using randomly varying seed values), even when applying very time-consuming optimization settings (e.g., maxiter = 100).

Best fit soVBGF parameter estimates with nearly unconstrained C (C varying from 0 to 1), using the search algorithm ELEFAN_GA varied strongly between runs, depending on the seed values used. “Best fit” \( L_\infty \) estimates were generally much lower than \( L_{\text{max}} \) (70 mm) and about half the optimal \( L_\infty \) of non-seasonal LFA with ELEFAN_GA (110.6 mm). Most of the “best fit” \( L_\infty \) estimates obtained for the soVBGF were below 55 mm, and 10 % of the “best fit” estimates were below 53.3 mm.
“Best fit” estimates for $L_\infty$ varied between 51.03 and 115.16 mm (mean: 67.98 mm, median: 55.11 mm), $K$ varied between 0.074 and 0.92 y$^{-1}$ (mean: 0.41 y$^{-1}$, median: 0.42 y$^{-1}$), and $C$ between 0.13 and 0.96 (mean: 0.57, median: 0.45). Rn scores varied from 0.25 to 0.39.

After 100 subsequent optimization runs (i.e., after 100 runs * 100 iterations = 10,000 iterations), the optimum (“best of the best”, with overall highest Rn score) soVBGF fit parameters $L_\infty$ and $K$ were very similar to the optimum parameters for non-seasonal VBGF growth. Optimum soVBGF parameters obtained with ELEFAN_GA were $L_\infty = 115.16$ mm, $K = 0.088$ y$^{-1}$, $C = 0.60$, $t_s = 0.575$, $t_{anchor} = 0.619$, $\Phi = 1.07 \log_{10}(y^{-1})+\log_{10}(cm)$ and a very high Rn score ($R_n = 0.389$).

The growth curves obtained with LFA, applying a fixed (or narrowly constrained) seasonal growth amplitude $C$ (derived from comparisons of mark-recapture increments between seasons), were very close to the to the optimum LFA results obtained with nearly unconstrained $C$. The combined use of several methods showed that an independent estimate of $C$, obtained from mark-recapture, could be successfully applied to LFA (see example in Fig. 3c). When applying a narrow search range for $C$, obtained from mark-recapture ($C = 0.47$ to 0.57), the soVBGF with ELEFAN_GA, with and all other parameters nearly unconstrained (i.e., searching within extremely wide search spaces, e.g. $L_\infty = 35$ to 1050 mm; $K = 0.01$ to 1 y$^{-1}$; $t_s = 0$ to 1), resulted in an optimum curve fit with a very large $L_\infty$ and very slow growth: with $L_\infty = 119.3$ mm; $K = 0.084$ y$^{-1}$; $t_{anchor} = 0.564$; $C = 0.514$; $t_s = 0.562$; $\Phi = 1.08 \quad 1.07 \log_{10}(y^{-1})+\log_{10}(cm)$ and a very high Rn score (0.383).
3.5. Bootstrapped mark-recapture analyses

Bootstrapped mark-recapture analysis with *grotag_boot* (*fishboot* package) was very time-efficient, with less than three minutes for 1,000 runs, with or without considering seasonality in growth. Median values of posterior distributions of $L_\infty$ and $K$ based on 1,000 runs were very close to the $K$ and $L_\infty$ estimates obtained from the original increments with the simple, non-bootstrapped *grotag* function. Median $L_\infty$ after bootstrapping was very large, far above $L_{\text{max}}$, and similar to the previous optimum value with $L_\infty = 118.1$ mm, (95% CI for $L_\infty$: 80.8 to 362.7 mm) and median $K$ was 0.121 y$^{-1}$, (95% CI for $K$: 0.024 to 0.26 y$^{-1}$), median $\Phi$’ was 1.24 log$_{10}$(cm+y$^{-1}$), (95%CI: 1.16 to 1.54 log$_{10}$(cm+y$^{-1}$)).

Including seasonality into mark-recapture analyses significantly reduced the precision of growth parameter estimates. Seasonal growth models were significantly less precise than non-seasonal growth models for $K$ ($p < 0.001$, interquantile range test) and for $\Phi$’ ($p = 0.024$, interquantile range test). However, for $L_\infty$, CI widths were not significantly different between seasonal and non-seasonal growth models (interquantile range test). Also, 95% CIs for the seasonal amplitude parameter "C" always included C = 0, and the median solution was always C = 0 ($C_{\text{median}} = 0.0$), indicating that the non-seasonal VBGF is the best model describing the combined mark-recapture data sorted along relative age (Fig. 2). After conducting 8,000 bootstrap resampling runs, 3,841 successful runs (48%) were obtained with useful random combinations of growth increments, where a VBGF could be fitted with *grotag_boot*. Among these, 1,000 results were randomly selected and used for further analyses and plotting (e.g., Fig. 2).
3.6. Bootstrapped length-frequency analyses

Bootstrap resampling from LFDs by using the \textit{ELEFAN\_GA\_boot} function (\textit{fishboot} package), produced useful results in all runs (n = 1,000). Length-frequency-based 95% CIs, obtained from \textit{ELEFAN\_GA\_boot}, were conspicuously and significantly wider (p < 0.0001 for all parameters, interquantile range test) than those obtained from tagging (Fig. 4). Tagging was approximately 3 times more precise than LFA for the estimation of the growth coefficient \(K\), and 2.2 times more precise for \(L_\infty\) (ESM Table 1). In spite of its higher complexity, the seasonal growth model was not more precise (p > 0.05 for \(K\), \(L_\infty\) and \(\Phi\), interquantile range test) than the simple non-seasonal VBGF. This is in opposition to mark-recapture results, where the non-seasonal growth model provided more precise results (i.e., narrower CIs).

For the optimum seasonal growth model, median amplitude C was 0.56 (very similar to estimates of C from non-bootstrapped LFA), indicating strong seasonal oscillations in growth. The 95% CI for C did not include C = zero (95% CI\(_C\): 0.15 to 0.93), indicating the existence of seasonality in growth, based on LFDs plotted at precise sampling dates. Median \(L_\infty\) for the bootstrapped soVBGF was 133 mm (95% CI\(_{L\infty}\): 50 to 673 mm) and median \(K\) was 0.10 \(y^{-1}\) (95% CI\(_K\): 0.01 to 0.73 \(y^{-1}\)), median \(\Phi\) was \(1.29 \log_{10}(cm+y^{-1})\), (95% CI\(_\Phi\): 0.93 to 1.93 \(\log_{10}(cm+y^{-1})\)).

Due to the complex genetic algorithms used for optimization, bootstrapped LFA was much slower than tagging-based analyses. Bootstrapped LFA with non-seasonal VBGF growth took approx. 5h per 1,000 runs, the full seasonal soVBGF models were even slower, with a duration
of approx. 20h per 1,000 runs. Furthermore, computation time was also affected by the amplitude of the search space (i.e., wideness of search ranges for K, \(L_\infty\) and C), and by the \textit{ELEFAN\_GA} precision-related parameters "maxiter", "run", and "pmutation", used for search optimization.

3.7. \textit{Bivariate confidence contour envelopes for K and \(L_\infty\)}

Bivariate confidence envelopes for growth parameters (\(L_\infty\) and K) always displayed a characteristic “banana shape”, \textit{i.e.}, the confidence contours were elongated, strongly bent and spread along a specific \(\Phi^\prime\) isopleth (Fig. 4). The confidence envelopes obtained from mark-recapture and LFA both followed this general shape, but with marked differences. Confidence envelopes derived from mark-recapture (\textit{grotag\_boot}) were conspicuously narrower for K ("flat" banana) than those derived from LFA (Fig. 4). Conversely, the shape of the confidence envelope derived from LFA (Fig. 4b) was relatively short for \(L_\infty\) and very tall for K, illustrating a much lower precision for K (3 times less precise than K obtained from tagging), but still within a conspicuous alignment along a specific \(\Phi^\prime\) isopleth (Fig. 4b).

3.8. \textit{Mortality estimates and their confidence intervals}

Total mortality \(Z\), as estimated by the common LCCC method, was 2.18 y\(^{-1}\) (Fig. 5a). This high mortality, combined with slow growth (e.g., \(K = 0.12\)) gives an extremely high \(Z/K\) ratio (\(Z/K = 18\)). This \(Z/K\) ratio of 18 is much higher (almost four-fold) than the \(Z/K\) ratio estimated by the widely used P-W method (e.g., \(Z/K_{\text{Powell-Wetherall}} = 4.2\)). Uncertainty in \(Z\), when estimated only by
the traditional regression-derived CI, was relatively low, with a relatively narrow CI (95% CI\(_Z\) = 1.7 – 3.1 y\(^{-1}\)). CI width from the common LCCC linear regression model was 3.1 - 1.7 = 1.4 y\(^{-1}\).

If the LCCC was a perfectly straight line, this CI width would be zero.

Each unique combination of growth parameters K and L\(_\infty\) (obtained from mark-recapture bootstrap, lower histogram in Fig. 5b), used as input for LCCC, produced a unique Z estimate. These Z posteriors (left histogram in Fig 5b) could be used to calculate 95% CIs for Z. This two-step bootstrap (orange dots and two histograms in Fig. 5b), considers uncertainty from the LCCC regression and uncertainty in original growth data (using posteriors from mark-recapture). This approach provided a wider 95% CI for Z (95% CI\(_Z\) = 1.5 to 3.5 y\(^{-1}\)), than when considering only the uncertainty derived from the LCCC regression model.

CI width obtained from the LCCC with two-step bootstrap was 3.5 - 1.5 = 2 y\(^{-1}\), considerably larger than CI width obtained from common LCCC only (Fig. 5). This method considers both sources of uncertainty (LCCC linear regression and steps prior to LCCC). Thus, for this population of *C. guanhumi*, 70% (100 * (1.4 / 2) = 70%) of the total uncertainty in mortality was derived from the LCCC linear regression model (i.e., from irregularities in the shape of the catch curve), while the remaining 30% (100 * ((2-1.4) / 2) = 30%) of the total uncertainty were derived from prior steps (i.e., determination of K and L\(_\infty\) by tagging).

The posterior distribution of Z/K ratios was calculated from randomly sampled pairs of bootstrap-derived posteriors of Z and K, thus considering uncertainty in Z and in K (95% CI\(_K\) =
0.024 to 0.26 y\(^{-1}\)), and non-linear error propagation. The median of the posterior distribution was \(Z/K = 18\), 95% CI \(Z/K = 7.5\) to 98. The application of bootstrap-based methods revealed a considerably higher \(Z/K\) ratio and a much higher uncertainty in \(Z/K\) (i.e., a larger CI width) than the traditional Powell-Wetherall plot method, using \(TropFishR\) (95% CI \(Z/K = 3.1\) to 4.9), showing the importance of using robust, bootstrapped methods.

Simulations (blue dots and gray triangles in Fig. 5b) with different simulated input growth parameters within a wide range (\(\Phi'\) from 0.5 to 2), showed a perfectly linear relationship between input \(\log(K)\) or \(\log(L_\infty)\) and output \(\log(Z)\), and between input \(\Phi'\) and output \(\log(Z)\) values (Fig. 5b). This shows that estimates of \(Z\) obtained with the LCCC method are log-linearly affected by any variations in \(\Phi'\), when using independent data sets for \(K\) and \(L_\infty\), with a slope of approximately 1: \(\log_{10}(Z) = -3.09 (+0.015) + \Phi' * 1.06 (+0.004), p < 0.0001, R^2 = 0.98\) (green dotted line in Fig. 5b).

4. Discussion

In this study, a new approach (the \textit{fishboot} R package) was applied to investigate a severely threatened land crab population, revealing slower growth, higher mortality and thus higher vulnerability to overharvesting than previously acknowledged. This is the first study to conduct bootstrapped analyses of mark-recapture growth increments and to compare the precision and uncertainty in tagging and LFA.
4.1. Unleash your algorithms - a plea for bootstrapped, unconstrained search

The first algorithms for length-based analysis of body growth, such as ELEFAN I (Pauly and Gaschütz, 1979; Pauly and David 1981) and MULTIFAN (Fournier et al., 1990) were created to improve earlier paper and pencil methods. There have been many advances since these first efforts, such as the recent “ELEFAN in R” (Pauly and Greenberg, 2013) and TropFishR packages (Mildenberger et al., 2017). Yet, the basic approach has remained the same since the very beginning: first, fix a single value for $L_{\infty}$ (based on $L_{\max}$ or on the P-W plot), then search for an optimum $K$ value.

Our results, based on two independent field methods (LFA and tagging), indicate severe shortcomings and dangerous pitfalls in these highly popular approaches and methods. Estimates for $L_{\infty}$ from traditional methods ($L_{\max} = 70$ mm, $L_{\infty,\text{Powell-Wetherall}} = 75.9$ mm) would provide much smaller estimates of asymptotic size than any $L_{\infty}$ estimates obtained from bootstrapped LFA and mark-recapture analyses. This confirms the conclusions of a recent simulation study (Schwamborn, 2018), that is not possible to fix or constrain $L_{\infty}$ \textit{a priori}, just by looking at the largest organism or by analyzing a catch curve with a P-W plot. Fixing $L_{\infty}$ \textit{a priori} by such dubious approaches has been widely used and was explicitly recommended by many authors (e.g., Gayanilo et al., 1997; Sparre and Venema, 1998; Schmalenbach et al., 2011; Taylor and Mildenberger, 2017), and may thus still be considered a current paradigm in fisheries science (Schwamborn, 2018). The present study shows that the uncertainty (i.e., the CI width) for $L_{\infty}$ may be much larger than previously thought, even when using an extremely accurate and reliable method for individual growth, such as mark-recapture with PIT tags.
The use of traditional LFA approaches for this *C. guanhumi* population would lead to an underestimation of $L_\infty$ and subsequent drastic overestimation of $K$, as in previous studies in this region. An extremely biased result would also have been obtained when simply using $L_{\text{max}}$ (70 mm) to assess $L_\infty$, or, even worse, “the average of the ten largest” (Wetherall et al., 1987), which would give an even lower $L_\infty$ ($L_{\text{average}10\text{max}} = 62$ mm) and erroneous subsequent calculations for growth and mortality. An underestimation $L_\infty$ and subsequent overestimation of $K$ by traditional LFA methods is what would be expected for a population with $Z/K$ ratio far above 2 (“Type B” population *sensu* Schwamborn, 2018). Clearly, $L_\infty$ should not be estimated from local $L_{\text{max}}$ and not be fixed prior to model adjustment. Instead, $L_\infty$, $K$, and their uncertainties should be simultaneously assessed, explicitly considering their strong interrelationship.

Furthermore, the $Z/K$ ratio obtained from tagging ($Z/K = 18$, 95%CI$_{Z/K}$: 7.5 to 98) was several times higher than any estimate with the P-W method ($Z/K$ estimates from 3.13 to 4.8). This confirms the severe bias in $Z/K$ estimates obtained from the P-W method, with data of a real population, as recently suggested by the simulations of Hufnagl et al. (2012) and Schwamborn (2018). One especially serious pitfall of the P-W method is the absurdly narrow 95% CI for $Z/K$ ratios (e.g. $Z/K_{\text{powell-Wetherall}} = 3.08$-$3.17$, using *TropFishR*), that will lead to a dangerous overconfidence in these clearly erroneous results.

Another dreadful pitfall of popular LFA methods is their susceptibility to become trapped at a local maximum of the multimodal response surface (Schwamborn et al., 2018b). In the present
study, repeated fit attempts with the modern curve fitting algorithm *ELEFAN_GA* (R package *TropFishR*) on the original land crab LFDs, applying different seed values (partial bootstrap *sensu* Schwamborn et al., 2018b), produced widely differing “best fit” VBGF parameters for each run, within a wide range of $L_\infty$ and $K$ values. An incautious analyst, using always the same seed value, would most likely have obtained always the same, unique “optimum” result at a specific local maximum in repeated analyses, leading to erroneous overconfidence in apparently perfect and replicable results. The present study thus highlights the importance of conducting large numbers of repeated analyses for all possible combinations of parameters, using explicitly different seed values (maximum stochasticity), and bootstrapping within complex, infinite, multidimensional, multimodal search spaces.

### 4.2. Comparison with previous studies of variability and uncertainty in body growth

Until now, there was no simple routine available to measure uncertainty in population-level estimates of body growth rates, based on tagging. Only few tagging-based studies have provided detailed accounts of the variability in growth (Wang, et al., 1995; Shakell et al., 1997; Zhang et al., 2009; Tang et al., 2014). Tang et al. (2014) used a complex hierarchical Bayesian model to analyze mark-recapture data from two species of freshwater mussels. They presented their $K$ and $L_\infty$ posteriors as a biplot, based on Monte Carlo simulations, but without constructing bivariate confidence contour ellipses. Thus, the present study is the first to use a non-parametric bootstrap for mark-recapture analysis and to present biplots with well-defined confidence contour envelopes, derived from tagging data.
In this study, bivariate posteriors (K and L\(\infty\)) were well aligned along \(\Phi'\) isopleths, and accordingly, \(\Phi'\) estimates in this study were very precise, for tagging and for LFA. This is probably a general phenomenon: even under ideal circumstances, it is probably impossible to obtain precise and accurate estimates for K and L\(\infty\), from LFA, due to their strong interdependence (higher K gives lower L\(\infty\) and vice-versa). At first sight, \textit{a priori} fixing L\(\infty\) by dubious methods seems to “miraculously” solve this problem, but this will inevitably lead to a huge underestimation of the overall uncertainty and to severe bias in L\(\infty\), K, Z, and Z/K, as shown in Schwamborn (2018) and in the present study. Thus, a “slim” banana-shape, is probably the best possible situation for LFD data, where estimates of K and L\(\infty\) are imprecise, but their interrelationship, described by \(\Phi'\), can be very precise.

Several studies have presented posterior distributions in the form of K vs L\(\infty\) biplots, also called “Kimura plots”, (Kimura, 1980, Kingsford et al., 2019), in studies based on tagging (Tang et al., 2014, this study), otolith readings (Villegas-Ríos et al., 2013; Goldstein et al., 2016; Kingsford et al., 2019), LFD data (Schwamborn et al., 2018b; Herrón et al. 2018, this study), and simulations with perfect LFDs (Schwamborn et al., 2018b, Schwamborn et al., 2019).

Three types of Kimura plots can be distinguished regarding the uncertainty in K, L\(\infty\) and \(\Phi'\):

Type 1: perfect length-at-age data, with little variability in K and L\(\infty\) will produce a well defined, narrow ellipse in the Kimura plot, based on excellent otolith-reading data, where all length and age classes are well represented, from early juveniles to the oldest individuals (Kimura, 1980;
Goldstein et al., 2016; Kingsford et al., 2019), Type 2: “banana-shaped” confidence envelopes, where uncertainty for $K$ and for $L_\infty$ is very high, but $\Phi'$ can be well assessed (Schwamborn et al., 2018b, Schwamborn et al., 2019, this study), and Type 3: “fried-egg-shaped” confidence envelopes derived from poorly structured LFDs (low pseudo-$R^2$ sensu Schwamborn et al., 2018b), as in Herrón et al. (2018), for Colombian Pacific fishes and for white clam ($Abra alba$) shell lengths in Schwamborn et al. (2018b).

The usefulness of $\Phi'$ has been intensively used to compare fish and other species since it was first proposed (Mathews and Samuel 1990, Živkov et al., 1999, Murua et al., 2017). Here, we provide additional evidence for the usefulness for $\Phi'$, especially regarding the observation that Type 2 Kimura plots (with “banana-shaped” confidence envelopes) seem to be the best possible situation in LFA, and probably for some tagging-based analyses, too (this study). Precision and accuracy for $K$ and $L_\infty$ in LFA is generally low, even for perfect synthetic LFD data (as in Schwamborn et al., 2019).

In the present study, the “banana” shape (Type 2 Kimura plot) obtained for $C. guanhumii$ LFDs, in spite of the extremely wide 95% CIs, was conspicuously different from the amorphous “fried egg”-shaped biplots (Type 3) produced with the same methods, for LFDs of three fish species by Herrón et al. (2018) and for the white clam $Abra alba$ by Schwamborn et al. (2018b). While in the present study, all biplots showed a unequivocal alignment to $\Phi'$ isopleths, in their data, there was no clear alignment of $K$ and $L_\infty$ posteriors along a specific $\Phi'$ isoline (no “banana“ shape), indicating a poor data structure (low signal/noise ratio and low “N”)

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Results from LFA in the present study showed a high level of uncertainty for K and $L_\infty$ (huge CIs), and were not as perfectly aligned along a single $\Phi'$ isoline as for the perfectly shaped, synthetic LFDs presented in Schwamborn et al. (2019) and as in the well-aligned mark-recapture growth estimates presented here. In the present study, the mark-recapture technique was 2.2 to 3 times more precise than LFA (narrower CIs for K and $L_\infty$), but even more remarkably, tagging also provided a better structure of the bivariate posteriors (posteriors were more narrowly aligned) resulting in narrower CIs for $\Phi'$.

4.3. Seasonality in growth

In spite of the general assumption of seasonality in growth, including for populations in the tropics (Pauly and Gaschütz, 1979; Pauly, 1987; Laslett et al., 2004), the present study is the first to perform statistical tests for seasonality in growth within bootstrapped analyses of growth. All tests confirmed the existence of significant seasonality in growth in C. guanhumi, in spite of a very small seasonal thermal amplitude in air temperature, of only 3.2 °C, in the tropical coastal region of Itamaracá.

A relationship between seasonal growth amplitude C and seasonal thermal amplitude $\Delta T$ has first been suggested by Pauly and Gaschütz (1979). This relationship was further analyzed by Pauly (1987), where $C = 0.11 \times \Delta T$. In the case of C. guanhumi in the Itamaracá mangroves, the expected value for C, considering only the thermal amplitude, would thus be $C = 0.11 \times 3.2 =$.
0.35. However, all our estimates of C, whether by comparing mark-recapture growth increments or by LFA with ELEFAN_GA or ELEFAN_GA_boot, resulted in considerably higher estimates for C (up to C = 0.6). It must be noted, however, that even Pauly (1987) suggested to use the estimates of C derived from ΔT as seed values for LFA only, not as conclusive values.

One reason for the large seasonal growth amplitude in *C. guanhumi* may be the observation that additionally to temperature, rainfall has a strong effect on the behavior and feeding of this species. These land crabs tend to be restrained inside their burrows during rainy periods, which obviously hampers their foraging activity. Thus, rather than being determined by temperature alone, seasonal feeding rhythms may be an important factor for these land crabs, such as for many other animals that have well-defined seasonal foraging rhythms. In many tropical coastal areas, seasonal factors other than temperature, such as rainfall and winds, may trigger changes in the environment and in the behavior of aquatic and land animals and thus in their growth rates. Another phenomenon, that certainly augments the seasonal growth oscillation in land crabs is the seasonal timing of the moulting cycle, with molts occurring predominantly in the dry season.

Considering the significant seasonality in growth, it may seem surprising, at first sight, that seasonal growth (soVBGF) was not an appropriate model for the description of mark-recapture increments, while for LFA the seasonal model was the most precise. This is derived from the fact that individual growth curves are not perfectly synchronous regarding their recruitment and seasonal timing. While each individual most likely has a seasonally oscillating growth curve, the overlap in time produces an “average” non-seasonal growth curve, based on rearranged mark-recapture growth increments, where these rearranged increments loose their seasonal time stamp.
(Fig. 2). This explains why the non-seasonal VBGF was significantly more precise for mark-recapture data than the soVBGF. The issue of strong overlap due to non-synchronous recruitment and growth probably also applies to length-at-age analyses derived from otolith readings, where non-seasonal growth models are still widely used (Villegas-Ríos et al., 2013; Goldstein et al., 2016; Kingsford et al., 2019).

Conversely, for the analysis of time series of monthly LFDs, seasonality can be explicitly plotted and modeled while adjusting the growth curve on the progressing monthly cohorts, that maintain their exact sampling date stamp during growth curve adjustment. This explains why the soVBGF was more precise (smaller CIs) than the non-seasonal growth model for LFA, in this study. Since the first applications, seasonal growth and mortality models have become widely accepted (Hufnagl et al., 2012). The approach to seasonality in the present study, with rigorous statistical tests, and combined tagging and LFA, is a further incentive for the use of soVBGF models and a further evidence of the usefulness of LFD data for seasonality analyses in stock assessment and population studies, even when other, more precise and accurate data, are also available.

4.4. Uncertainty in mortality estimates – consequences for stock assessment

This study showed that the total mortality $Z$ is strongly and log-linearly influenced by input $\Phi'$ values ($R^2 = 0.98$). The LCCC method seems to be robust to errors and variations in $K$ and $L_{\infty}$, as long as lower $K$ values lead to higher $L_{\infty}$, within slender $\Phi'$ isopleths, which is common for
highly informative data (see above). Our simulations showed that Z was dependent on L∞, K, and Φ’ when using independent data sets of K and L∞. Thus, when L∞ and K are not aligned along a Φ’ isopleth (Type 3 bivariate datasets, e.g., poorly structured LFD data), any errors in estimates of L∞ (or in K) will affect the subsequent LCCC estimation of mortality directly (by the direct effect on the LCCC method). For Type 2 datasets, error in L∞ will be compensated by its effect on K, with constant Φ’ and thus probably have little effect on the LCCC method. To ignore the uncertainty in underlying growth estimates and error propagation may lead to an underestimation in CI width for Z, which is a key parameter for any population studies or stock assessments.

In this study, with well-structured growth estimates (“Type 2” data pairs) obtained with PIT tags, 95% CI width of Z was very narrow (giving a precise estimate for Z), due to the compensatory nature of K and L∞ errors within LCCC (see above). Furthermore, only 30% of the overall uncertainty in Z for the C. guanhumi population in Itamaracá was derived from error propagation from growth estimates, the remaining 70% being due to the uncertainty that is intrinsic of the LCCC linear regression model, due to irregularities in the shape of the catch curve and the number of size classes used for regression. When using less precise growth estimates, such as those derived from LFA, the percentage or error in Z derived from growth (i.e., from the initial estimates) in a complete evaluation is most likely much higher. This further highlights the need to acknowledge these sources of error, instead of only looking at the parametric error terms of the linear regression model, as done in most current analyses and popular stock assessment software tools.
In Itamaracá island, Z values for *C. guanhumi* were much higher and CI width was much wider than reported for mangrove crabs *Ucides cordatus* in Pará state (Northern Brazil), investigated by Diele and Koch (2010). Extremely precise estimates for Z were obtained for *U. cordatus* in Pará, using LCCC: 0.69 ± 0.077 (95% CI) for males and 0.49 ± 0.086 (95% CI) for females (Diele and Koch, 2010). These extremely narrow CIs are probably due to the “textbook” log-linearity of the *U. cordatus* catch curves and the fair numbers of large-sized mangrove crabs, providing many degrees of freedom for the linear regression model. Furthermore, the 95% CIs given by Diele and Koch (2010) did not consider the uncertainty derived from the underlying growth model.

Estimates of instantaneous natural mortality M (by definition, when there is no fishing, M = Z) obtained in the present study (Z = 2.2 y⁻¹, 95% CI = 1.7 to 4.5 y⁻¹), can be considered to be extremely high, since published estimates of M for fish and large crustaceans such as crabs and lobsters are generally below 1 y⁻¹, and values above M = 1 y⁻¹ are already considered to be high mortalities (Then et al., 2015; Costa et al., 2018). The 95% CI included values from high (Z = 1.7 y⁻¹) to extremely high (Z = 4.5 y⁻¹) mortality. Even with a very careful analysis and considering several sources of uncertainty, the 95% CI for mortality did not include a possibility of low mortalities (e.g., values of Z < 1), which indicates that this population is in a critical situation, even when considering the uncertainty in the methods and analyses used. Other simple indicators of unsustainably high mortality are that no old animals were found, all were very small animals, well below L∞, and that no ovigerous females were found. The latter observation indicates that recruitment is derived from past reproduction events or that recruits in Itamaracá are derived from allochthonous larval production.
4.5. *Spurious autocorrelation in popular meta-analyses - from growth to mortality and back*

Our simulations showed that variations in input $K$, $L_x$, and $\Phi'$ will directly affect the output estimate of $Z$. This may have severe, hitherto unacknowledged consequences for widely used estimates of natural mortality. Since the first attempt to predict natural mortality from mean temperature, $K$ and $L_x$ (Pauly, 1980), numerous similar “empirical” models (Gulland 1987; Hoenig, 1983; Charnov, 1993; Jensen, 1996; Jensen, 2001; Hewitt and Hoenig, 2005; Gislason et al., 2010; Then et al., 2015) have been proposed that allow to predict natural mortality of a given population from input data of growth parameters, maximum size, or maximum age ($t_{\text{max}} = t_0 + 3 / K$, Taylor, 1958). However, many (if not all) published mortality estimates have been obtained by methods that depend directly on growth parameters and body size as input. Any attempt to conduct a linear regression analysis of mortality vs growth will therefore give statistically significant results, not because of supposedly relevant ecological or physiological phenomena, but solely because of the lack of independence between “$X$” and “$Y$” in the underlying regression model. Such spurious autocorrelation artifacts will afflict any quantitative study, when non-independent variables are used in regression models. Spurious autocorrelation was recognized as an extremely serious issue for quantitative science since the very first linear regression models (Pearson, 1897; Reed, 1921; Brett, 2004; Auerswald et al., 2010; Schwamborn, 2018). Thus, it is imperative that previously published and widely used models that attempt to predict mortality from body growth and size, should be carefully reassessed for potential autoregressive artifacts.
4.6. Comparison with other C. guanhumi populations

At first sight, the “dwarfed” size distribution of giant land crabs observed at Itamaracá island ($L_{\text{max}} = 70$ mm) could seem to be a particularly dramatic case. However, a quick survey of regional literature on this species shows that such small-sized $C. \text{guanhumi}$ populations are very common in the tropical mangroves of northeastern Brazil. Several studies reported size distributions for northeastern Brazilian $C. \text{guanhumi}$ populations that are similar or even smaller ($L_{\text{max}} = 62$ mm, Botelho, et al., 2001) than in the present study, sampled in mangroves in Pernambuco (Botelho et al., 2001), Paraíba (Takahashi 2008), Rio Grande Norte, (Silva, 2013, Silva et al., 2014) and Ceará (Shinozaki-Mendes et al., 2013). Thus, the “dwarfed” $C. \text{guanhumi}$ population analyzed in this study can be considered typical for this species in this region. Yet, in other regions, “giant” specimens do occur. In the considerably colder climate of subtropical southeastern Brazil, where $C. \text{guanhumi}$ is not commercially exploited, large-sized animals have been reported, with $L_{\text{max}}$ values reaching 94 mm in São Paulo State (Gil, 2009).

The present study differs from earlier attempts to assess body growth in $C. \text{guanhumi}$ (Botelho et al., 2001), mainly in that all $L_{\infty}$ estimates obtained here are much larger than any individuals of this species ever reported from northeastern Brazil. This large $L_{\infty}$ estimate would seem suspicious in the eyes of any local analysts or ecosystem managers, who generally consider local or regional populations only. Looking only at previously reported $L_{\text{max}}$ and length-based $L_{\infty}$ values reported from this region with extremely overharvested populations, would lead to the erroneous conclusion that the large $L_{\infty}$ estimates (generally above 100 mm) obtained by mark-recapture in this study are unrealistic and thus incorrect. However, a wide-scale search proves
that global L\textsubscript{max} for this species is far above local L\textsubscript{max} at Itamaracá Island (70 mm), especially when including pristine populations found in other regions. The L\textsubscript{\textinfty} estimates obtained in the present study are close to L\textsubscript{max} values reported from other regions, such as Florida (L\textsubscript{max} = 102 mm, Herreid, 1963), Mexico (L\textsubscript{max} = 105 mm, Bozada and Chávez, 1986, ) and Cuba (L\textsubscript{max} = 105 mm, Rivera, 2005), where this species is not commercially caught. A quick search in SeaLifeBase (Palomares and Bailly, 2011) yields an even larger L\textsubscript{max} value (L\textsubscript{max} = 150 mm), based on evidence from Florida (Hostetler \textit{et al.}, 2003), together with another very large L\textsubscript{max} value of 120 mm reported from Puerto Rico (Forsee and Albrecht, 2012). Thus, to widen the search radius (in time and geographically) may help to open the perspective and to perceive the potential of any given species for its global maximum size. This may be helpful in defining plausible L\textsubscript{\textinfty} ranges in data-poor situations, especially for severely overfished and threatened populations, where current L\textsubscript{max} values are drastically reduced (Schwamborn, 2018).

4.7. Factors of mortality in land crabs

Several factors may have contributed to the observed high mortalities in land crabs. Unsustainable harvesting by artisanal fishermen is a key aspect in this region, especially considering that harvesting of mangrove crabs (e.g., \textit{Ucides cordatus}, \textit{Goniopsis cruentata} and \textit{C. guanhumi}) is the single most important source of income for the poorest fishermen in coastal communities in northeastern Brazil (Schwamborn and Santos, 2009; Firmo \textit{et al.}, 2012). Yet, this aspect is possibly of lesser importance in closed areas (Silva, 2013; this study), although occasional, illegal intrusions of fishermen in such areas may have occurred at some point in the years that preceded this study.
The most likely explanation for high Z is intensive predation by small mammals, such as stray dogs, stray cats, rats, crab-eating racoons (*Procyon cancrivorus*), opossum (*Didelphis* sp.), monkeys, and crab-eating foxes (*Cerdocyon thous*), all of which are very common in this study area (Moraes-Costa and Schwamborn, 2018) and known to feed on mangrove crabs. Empty carapaces of *C. guanhumi* and other evidences of feeding by small mammals are abundant in the study area (Moraes-Costa and Schwamborn, 2018). Predation mortality caused by small mammals, although not related to fisheries, can hardly be called “natural“ mortality, since these predator populations are either introduced by humans (rats, stray pets, etc.) or positively affected by the removal of larger predators (large felines) by humans. Another possible explanation for high crab mortalities can be diseases, such as the epidemic of yeast-like fungi of the family *Herpotrichiellacea* in 2004-2005, although such fungal pathogens have hitherto only been observed in crabs of the species *Ucides cordatus* (Vicente et al. 2012). Pesticides and other pollutants are probably also relevant in the context of crab mortality, especially considering that mangroves are commonly used as disposal sites for sewage, solid waste and numerous toxic chemicals (Yogui et al., 2018; Santos et al., 2019). The importance of harvesting by local fishermen for the population structure of *C. guanhumi* cannot be overstated, even in closed areas. This is especially evident when comparing the size structure of this species in northeastern Brazil and in regions where this species is not regularly harvested (see above).
4.8. Conclusions and Outlook

Most management decisions still assume the existence of unique, precise estimates of K, $L_\infty$, and Z, even when there is a high variability in the underlying data, and consequently, there is considerable uncertainty in growth and mortality estimates obtained. Under such circumstances, doubtful approaches are often used for curve fitting (e.g., \textit{a priori} fixing $L_\infty$). Instead, the present study highlights the importance of developing new management tools for data-poor stocks, that explicitly acknowledge the uncertainty in K and $L_\infty$ within multi-step, bootstrapped analyses.

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Figure 1. Length-frequency distributions of 1,078 individuals of blue land crabs (C. guanhumi) caught in the Itamaracá mangroves, Brazil. above: raw length-frequency distributions (black bars) with cohorts detected by the Bhattacharya method (green dots). below: restructured data with MA = 7. CW: carapace width.
Figure 2. Growth curves for blue land crabs (*C. guanhumi*) in the Itamaracá mangrove, Brazil, obtained by traditional length-frequency analysis (red) and with bootstrapped marc-recapture data (green line with gray envelope). Continuous green line: VBGF curve with “best fit” parameters obtained by mark-recapture ($L_\infty = 108.03$ mm, $K = 0.145$ y$^{-1}$), based on 130 size increments of tagged individuals. Blue dashed curves and grey area: 95% confidence envelope obtained by bootstrapping, based on marc-recapture data. Red dashed line: Previous VBGF curve, obtained with common length-based methods (Powell-Wetherall plot and K-scan, $L_\infty = 72.5$mm, $K = 0.38$ y$^{-1}$).
Figure 3. Seasonality in recruitment and growth of blue land crabs (*C. guanhumi*) in the Itamaracá mangroves, Brazil. a.) Seasonality of recruitment (%). b.) Seasonal variation of growth increments (dL/dt) obtained by mark-recapture. Lines: general additive model (GAM). c.) Example of a seasonally oscillating soVBGF growth curve ($L_\infty = 107.1$ mm, $K = 0.135$ y$^{-1}$, $C = 0.53$, $t_{anchor} = 0.70$, $ts = 0.22$, $Rn = 0.28$). Growth parameters were obtained by using the “best fit” parameters obtained by mark-recapture as seeds for final adjustments using ELEFAN_GA.
Figure 4. Uncertainty in growth parameters $K$ and $L_\infty$ for blue land crabs (*C. guanhumi*) in the Itamaracá mangroves, Brazil. 
a.) Uncertainty in growth parameters $K$ and $L_\infty$ based on tagging (130 growth increments). b.) Uncertainty in growth parameters $K$ and $L_\infty$ based on length-frequency analyses with ELEFAN I (1,078 individuals), $n = 1,000$ bootstrap runs for both methods. Outer contour: 95% confidence envelope. Grey lines: $\Phi'$ isopleths.
Figure 5. Uncertainty in total mortality (Z) of blue land crabs (C. guanhumi), tagged with PITs in the Itamaracá mangroves, Brazil. a.) Length-converted catch curve (LCCC) used to estimate total mortality (Z) and 95% Confidence interval calculated from linear regression analysis during LCCC. b.) Estimation of uncertainty in total mortality (Z) by three different approaches: i.) 95% confidence interval obtained from LCCC. ii.) 95% confidence interval based on two-step Bootstrap, i.e., on repeated analysis using posteriors (1,000 pairs of K and L∞) obtained from bootstrapped tagging analysis. i+ii.) uncertainty from both sources. Blue circles, grey triangles and dotted green line: simulation study using 1,000 random uniform values for K and L∞ and subsequent LCCC analysis. Blue circles: central estimate for Z from LCCC, for each simulation. grey triangles: 95% conf. intervals for Z in each simulation. CI: confidence interval.
**ESM Table 1.** Growth and mortality parameters obtained for blue land crabs (*C. guanhumi*) in the Itamaracá mangroves, Brazil, by length-frequency analysis (LFA), or by tagging with Passive Integrated Transponder (PIT) tags. CW: carapace width; LCCC: Length-converted catch curve. CI: 95% confidence interval.

| Method | Asymptotic size $L_\infty$ (CW, mm) | Growth coefficient $K$ (y$^{-1}$) | $\Phi'$ (log$_{10}$(cm y$^{-1}$)) | Seasonal amplitude $C$ | Total Mortality $Z$ (y$^{-1}$) | $Z/K$ ratio |
|--------|-----------------------------------|-----------------------------------|---------------------------------|-----------------------|-----------------------------|-------------|
| Powell-Wetherall plot (FISAT II), LFA | 75.9 mm | - | - | - | - | 4.2 |
| Powell-Wetherall plot (TropFishR), LFA | 69.3 to 75.9 mm (95%CI: 48.9 to 119.2 mm) | - | - | - | - | 3.1 to 4.8 (95%CI: 3.1 to 4.9) |
| $K$ scan (FISAT II), LFA ($L_\infty$ = 75.9, fixed) | fixed | three optima: 0.15, 0.21, 0.38 | 0.98, 1.12, 1.38 | - | - | - |
| RSA (FISAT II & TropFishR), LFA | 72.5 mm | 0.38 | 1.30 | - | - | - |
| ELEFAN_GA, non-seasonal (TropFishR), LFA | 110.6 mm | 0.094 | 1.06 | - | - | - |
| ELEFAN_GA_boot, seasonal growth (C = 0 to 1), simple repeated fits (partial bootstrap), nruns = 100 (fishboot), LFA | 115.2 mm | 0.088 | - | - | - | - |
| ELEFAN_GA_boot, seasonal growth (C = 0 to 1), full non-parametric bootstrap, nruns = 1000 (fishboot), LFA | median: 133 mm (95%CI: 50 to 733 mm) | median: 0.1 to 0.73 | median: 1.25 to 1.98 | median: 0.6 to 1.5 (95%CI: 0.15 to 0.93) | - | - |
| Mark-recapture with grotag, non-seasonal VBGF (fishmethods), PIT | 108.03 mm | 0.145 | 1.23 | - | - | - |
| Mark-recapture with grotag_boot, non-seasonal VBGF, nruns = 1000 (fishboot), PIT | median: 118.1 mm (95%CI: 80.8 to 362.7 mm) | median: 0.121 to 0.024 to 0.26 | median: 1.23, 0.95 (95%CI: 0.86 to 1.36) | - | - | - |
| LCCC (TropFishR), PIT | - | - | - | 2.18 (95%CI: 1.7 to 3.1 y$^{-1}$) | - | - |
| LCCC with two-step bootstrap (fishboot), PIT | - | - | - | 2.19 (95%CI: 1.5 to 3.5 y$^{-1}$) | - | - |
| $Z/K$ ratio. Calculation: $K$ from tagging, $Z$ from LCCC | - | - | - | 18 (95%CI: 6.9 to 188) | - | - |