Evaluation of three length-based methods for estimating growth in tropical fishes: The red snapper
*Lutjanus campechanus* of the Campeche Bank (Mexico)*

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SUMMARY: Growth of the red snapper *Lutjanus campechanus* off the Campeche Bank was estimated by the length-based methods ELEFAN, SLCA and PROJMAT, the last two applied for the first time to this resource. The jackknife technique was applied to deal with uncertainty in growth estimates resulting from chance variations in sampling design. Results differed among methods: ELEFAN overestimated $L_\infty$, whereas PROJMAT and SLCA gave parameter estimates within the range reported in the literature. Results derived from jackknife analysis revealed lowest variability in the precision estimators -percent error and coefficient of variation- when applying SLCA and PROJMAT. Estimates of the comparative growth index $\phi'$ agreed with those observed for different geographic regions (between 2.92 and 3.19), except for ELEFAN. We suggest to abandon the use of the ELEFAN method in favour of recently developed SLCA and PROJMAT.

Key words: Growth, length-based methods, jackknife, uncertainty, *Lutjanus campechanus*, Campeche Bank.

RESUMEN: EVALUACIÓN DE TRES MÉTODOS INDIRECTOS PARA ESTIMAR EL CRECIMIENTO EN PECES TROPICALES: EL HUACHI-NANGO *Lutjanus campechanus* DEL BANCO DE CAMPECHE (MÉXICO). – En este trabajo se estimó el crecimiento del “huachinango” *Lutjanus campechanus* del Banco de Campeche (México) en base al análisis de frecuencia de tallas por medio de los métodos ELEFAN, PROJMAT y SLCA, los dos últimos por primera vez aplicados a este recurso. Se cuantificó la variabilidad de los estimadores y el efecto de las muestras mensuales a través de la técnica de remuestreo jackknife. Los resultados fueron disímiles: el ELEFAN sobreestimó $L_\infty$ con respecto a los valores reportados en la literatura, mientras que el PROJMAT y SLCA aportaron valores dentro del rango observado. La aplicación del jackknife mostró mínimos valores de los estimadores de precisión -coeficiente de variación y error porcentual- con SLCA y PROJMAT. Los intervalos del índice comparativo de crecimiento $\phi'$ coincidieron con los observados para la especie en diferentes regiones geográficas en los dos últimos métodos mencionados (entre 2.92 y 3.19). Por tanto, se sugiere abandonar el uso del ELEFAN, técnica comúnmente empleada en este recurso tropical, en favor de los métodos más recientemente desarrollados SLCA y PROJMAT.

Palabras clave: Crecimiento, métodos indirectos, jackknife, incertidumbre, *Lutjanus campechanus*, Banco de Campeche.

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INTRODUCTION

Age in fishes has traditionally been estimated by counting growth rings in hard structures (e.g., bones, otoliths and scales). The technique has been developed and most used in temperate areas, where marked seasonal variations in environmental parameters and relatively short spawning periods are typical. In tropical environments, characterized by less variable climatic conditions and extended spawning seasons, age estimates are more difficult to obtain, because growth rings often overlap or show indistinct boundaries (Lowe-Mcconell, 1987).

In addition to difficulties in counting growth rings from the tropics, the protracted reproductive season and concomitant period of recruitment complicates the interpretation of progression analyses based on modes of length frequency distributions (LFDs), because there is often no clear seasonal peak in LFDs (Morales-Nin, 1992). Samples taken from only a particular part of an extended reproductive season may also be subjected to environmental or random variations, yielding values not representative of the entire season. Moreover, growth studies in fishes - in both temperate and tropical species - are usually based on samples obtained from commercial catches, which, because of gear selectivity, may not be representative of the overall population (Mathews, 1974; Morgan, 1983).

These problems may introduce biases, and increase uncertainty in the estimation of population growth parameters, especially for tropical fishes. To provide precise growth estimates it is necessary to quantify: (1) the effect of random variations in data; (2) the relative importance of divergent samples that compose a data set; and (3) the uncertainty in growth parameters around mean estimates (Gulland and Rosenberg, 1992). Comparison of standard growth indices derived from different analytical techniques (Vakily, 1990) is also useful in evaluating the precision of different estimates of growth parameters.

The red snapper, *Lutjanus campechanus* Poey 1860, is mainly distributed in the tropical waters of Campeche Bank, southern Gulf of Mexico. Although the species is of commercial importance, information about age and growth is scarce: González (1988) estimated growth by counting rings in scales, but was not able to validate the period of ring formation. She also used an early version of the ELEFAN Program (Electronic Length Frequency Analysis: Pauly and David, 1981) to analyze LFDs without giving estimates for goodness of fit (e.g., ESP/ASP ratio, see below) for the derived growth curve.

Since LFDs are relatively easy to obtain, growth estimates are routinely based on them, and analytical procedures have been developed to derive estimates of growth parameters from these distributions. Three of the most popular procedures are Electronic Length Frequency Analysis (ELEFAN) (Gayanilo et al., 1994), Projection Matrix Method (PROJMAT) (Shepherd, 1987a; Rosenberg et al., 1986) and Shepherdiís Length Composition Analysis (SLCA) (Shepherd, 1987b). In this setting, it is necessary to evaluate the relative merits of each analytical procedure, as well as to test the effects of sources of uncertainty in the data. Thus, the main objectives of the present work involved: (a) estimating growth parameters of *L. campechanus* off the Campeche Bank, using ELEFAN, PROJMAT and SLCA; (b) quantifying uncertainty in model parameters resulting from variations in input data (i.e. each sample that comprise the data set); and (c) comparing the new estimates with those previously reported, through the standard growth index $\phi'$ (Vakily, 1990).

MATERIALS AND METHODS

Red snappers were sampled monthly during 1992 from commercial landings of the mechanized fleet at the ports of Yucalpetén and Progreso, Yucatán State, México. A total of 5,690 red snappers ranging from 24 to 93 cm of total length ($TL$) were sampled and measured with 1 mm precision, and the resulting Length Frequency Distributions (LFDs) grouped in size intervals of 2 cm. Fork lengths ($FL$) were transformed to $TL$ by:

$$TL = 1.1093 - FL^{0.9864}$$

(n= 238; $r^2= 0.99; p<< 0.01$), to compare our growth estimates with those reported in the literature.

The length-based methods (ELEFAN, PROJMAT and SLCA), which assume that growth follows the von Bertalanffy growth equation (Defeo et al., 1992), were used for parameter estimation:

1. ELEFAN Program identifies peaks and troughs in the LFDs and fits a growth curve passing through a maximum number of peaks. It does not assume normality for the LFDs (see Gayanilo et al., 1994 for details). An index of goodness of fit, called Rn, is determined by:
where ESP stands for the “Explained Sum of Peaks” and ASP for “Available Sum of Peaks”.

(2) PROJMAT, based on the Leslie population projection matrix (Leslie, 1945), projects one sample of the LFD from time $t$ to time $t+1$, using seed values of $K$ and $L_{\infty}$. The projected LFD is compared with the observed LFD through the sum of squared differences (SSQ). This procedure is repeated over all comparisons between $n$ samples for a range of $K$ and $L_{\infty}$ values, where the best estimates are which minimize the SSQ (Basson et al., 1988).

(3) SLCA is based on a cosine function independent of the number and position of the modes:

$$
T(l) = \frac{\sin \Pi (t_{\text{max}} - t_{\text{min}})}{\Pi (t_{\text{max}} - t_{\text{min}})} \cos 2 \Pi (t_{\text{avg}} - t_s)
$$

where $t_{\text{max}}$ and $t_{\text{min}}$ are, respectively, ages-at-length corresponding to the upper and lower bounds of a given length interval, $t_{\text{avg}}$ is the average age, and $t_s$ is the fraction of the year in which the sample was taken (Shepherd, 1987b). A test function of the form:

$$
S = \sum \sum T(l,i) \sqrt{N_{li}}
$$

is maximized by the most appropriate combination of growth parameters, where $l$ indexes the length groups, $i$ indexes the available LFDs and $N$ is the observed frequencies (Jones et al., 1990).

The jackknife technique was applied to quantify the effect of input data variations in growth parameter estimates (Levi et al., 1987). Thus, each of the 12 samples was sequentially omitted with substitution; 12 groups of 11 data were generated, thus providing 12 different combinations of growth parameters. The percent error (PE) and the coefficient of variation (CV) were used as precision estimates. The former was obtained as:

$$
PE = \frac{(St - St_j) \times 100}{St_j}
$$

where $St$ is the growth parameter estimate using the complete data set (12 months), and $St_j$ is the mean parameter estimate coming from the $n$ jackknife “pseudovalues”. PE is optimum when equal to 0 ($St=St_j$). The jackknifed CV was obtained by:

$$
CV = \frac{\sqrt{\sum (St_{i-1} - St_j)^2}}{n(n-1)} \times 100
$$

where $St_{i-1}$ is the parameter estimate when omitting a particular sample and $n$ is the sample size (12).

The standard growth index $\phi'$ (Pauly and Munro, 1984; Vakily, 1990) was used as a criteria to compare different parameter estimates:

$$
\phi' = 2 \log_{10}(L_{\infty}) + \log_{10}(K)
$$

$\phi'$ was estimated for each pair of $K$ and $L_{\infty}$ obtained with the whole data set, as well as for those resulting from jackknife analysis. Results were compared with those $\phi'$ values coming from $K,L_{\infty}$ estimates reported in the literature.

RESULTS

The complete data set

The three length-based analytical techniques produced similar results for $K$, but drastically different predictions for $L_{\infty}$ and moderately different results for $t_s$ (Table 1). Thus, although the calculated rates of growth were comparable for the three methods, the length-at-age predictions for ELEFAN were more than twice those provided by either PROJMAT and SLCA. In addition, the goodness of fit index for ELEFAN was notably low ($R_n = 0.18$), further indicating poor explanatory power of this model. In contrast, PROJMAT and SLCA produced identical estimates for $K$, and similar values for $L_{\infty}$ (Table 1).

Jackknife analysis

Jackknife iterations, sequentially omitting one of 12 months of data, showed different effects of chance variations in input data between the three analytical techniques (Fig. 1). In the case of ELEFAN, $L_{\infty}$ varied from 223 to 300 cm TL (25.6%), while $K$ ranged...
from 0.12 to 0.18/year. Both parameters were significantly correlated ($r^2=0.63$; $p<0.01$). There was a notable negative progression from January to December: the highest $L_\infty$ and lowest $K$ values occurred when January was omitted, while the lowest $L_\infty$ and highest $K$ values were produced when December was omitted (Fig. 1A). Jackknife iterations with PROJMAT yielded a similar level of spread in estimates of $K$ (0.11 to 0.17/year), but considerably less variation in the estimates of $L_\infty$ (94 to 112 cm TL; 14.3%). There was no predictable relation between both parameters. Despite generally less variable results, estimates when omitting October were considerably greater than for the other eleven data sets ($L_\infty = 112$ cm TL and $K = 0.17$/year) (Fig. 1B). The SLCA model produced the lowest variation in both $K$ (0.13 to 0.17/year) and $L_\infty$ (81 to 87 cm TL; 6.9%). Both parameters were strongly cross-correlated ($r^2=0.93$; $p<<0.01$) (Fig. 1C).

Analysis of precision estimates derived from jackknife analysis showed that SLCA consistently produced the lowest PE and CV values for all three growth parameters. ELEFAN yielded by far the highest PE for both $K$ and $L_\infty$ and the highest CV values for all three growth parameters, whereas results from PROJMAT were generally intermediate between these other two models (Table 1).

| TABLE 1. – Growth parameters ($L_\infty$: cm TL, $K$: 1/yr and $t_o$: yr) of $L$. campechanus from the Campeche Bank, Mexico, estimated by ELEFAN, PROJMAT and SLCA. Estimates were produced from the entire 12-month sample (St), as well as from the average of 12 jackknife iterations, sequentially removing one month’s data (Y); precision estimates included percent error (PE) and coefficient of variation (CV); goodness of fit indices for ELEFAN ($R_n$), the sum of squared differences (SSQ) for PROJMAT and the $S$ score for SLCA are shown. |
|---|---|---|---|
| | ELEFAN | PROJMAT | SLCA |
| $L_\infty$ | St | 285 | 104 | 85 |
| | Y | 262 | 102 | 85 |
| PE(%) | St | 8.55 | 1.96 | 0.39 |
| | Y | 2.60 | 1.82 | 0.46 |
| $K$ | St | 0.13 | 0.14 | 0.14 |
| | Y | 0.15 | 0.14 | 0.14 |
| PE(%) | St | 11.86 | 0.00 | 0.00 |
| | Y | 3.83 | 3.43 | 2.22 |
| $t_o$ | St | -0.19 | -0.23 | -0.31 |
| | Y | -0.28 | -0.47 | -0.35 |
| PE(%) | St | 31.12 | 51.00 | 12.85 |
| | Y | 17.29 | 16.53 | 11.17 |
| Goodness of fit | $R_n=0.18$ | SSQ=0.62 | $S = 1$ |

Fig. 1. – Relationship between $L_\infty$ and $K$ in $L$. campechanus from the Campeche Bank (Mexico), estimated by (a) ELEFAN; (b) PROJMAT; and (c) SLCA. Each letter refers to the month omitted in jackknife analysis.
Comparisons with the standard growth index $\phi'$

Consistently higher ELEFAN estimates of $L_\infty$ in the jackknife iterations determined the highest $\phi'$ values (close to 4). PROJMAT values for $\phi'$ were slightly higher than those obtained by SLCA. The sequential omission of samples yielded ELEFAN $\phi'$ values varying between 3.91 (June omitted) and 4.08 (October omitted); PROJMAT $\phi'$ values ranged from 3.06 (August omitted) to 3.30 (October omitted). SLCA $\phi'$ values were notably consistent and close to 3.00 throughout the twelve calculations (Fig. 2).

Growth parameters calculated from other studies carried out in more northern areas were comparable to the results of the present investigation using the two length-based models SLCA and PROJMAT (Table 2). The $\phi'$ values, calculated from published $L_\infty$ and $K$ values reported from these previous studies, varied between 2.92 and 3.19, a range that includes the $\phi'$ values produced by SLCA and PROJMAT (3.00 and 3.18). Remarkably, the $L_\infty$ and $\phi'$ values resulting from the ELEFAN method was well outside the range of values resulting from studies based on counts of growth rings (Fig. 2).

![Graph](image)

**Fig. 2.** – *L. campechanus*. Monthly variations of $\phi'$ resulting from estimates of $L_\infty$ and $K$ shown in Fig. 1. The solid horizontal lines A, B and C indicate, respectively, maximum, mean and minimum $\phi'$ estimates derived from the age-length key given by Leonce-Valencia (1995).

**Table 2.** – Growth parameters of *L. campechanus* reported in the literature for different geographical regions. $L_\infty$ refers to total length (TL).

<table>
<thead>
<tr>
<th>Area</th>
<th>Method</th>
<th>$L_\infty$ (cm)</th>
<th>$K$ (1/yr)</th>
<th>$\phi'$</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Louisiana (USA)</td>
<td>SO</td>
<td>95.0</td>
<td>0.18</td>
<td>3.19</td>
<td>Nelson and Manooch (1982)</td>
</tr>
<tr>
<td>W Florida (USA)</td>
<td>SO</td>
<td>94.1</td>
<td>0.17</td>
<td>3.17</td>
<td>Nelson and Manooch (1982)</td>
</tr>
<tr>
<td>E Florida (USA)</td>
<td>SO</td>
<td>97.0</td>
<td>0.16</td>
<td>3.17</td>
<td>Nelson and Manooch (1982)</td>
</tr>
<tr>
<td>Gulf of Mexico</td>
<td>SO</td>
<td>94.0</td>
<td>0.17</td>
<td>3.17</td>
<td>Nelson and Manooch (1982)</td>
</tr>
<tr>
<td>Carolinas (USA)</td>
<td>SO</td>
<td>97.0</td>
<td>0.17</td>
<td>3.19</td>
<td>Nelson and Manooch (1982)</td>
</tr>
<tr>
<td>Gulf of Mexico</td>
<td>SO</td>
<td>92.5</td>
<td>0.14</td>
<td>3.07</td>
<td>Nelson et al. (1985)</td>
</tr>
<tr>
<td>Tamaulipas</td>
<td>BP</td>
<td>80.4</td>
<td>0.13</td>
<td>2.92</td>
<td>Rodríguez (1992)</td>
</tr>
<tr>
<td>Campeche Bank</td>
<td>S</td>
<td>95.0</td>
<td>0.13</td>
<td>3.06</td>
<td>González (1988)</td>
</tr>
<tr>
<td>Campeche Bank</td>
<td>ELEFAN</td>
<td>90.0</td>
<td>0.13</td>
<td>3.02</td>
<td>Leonce-Valencia (1995)</td>
</tr>
<tr>
<td>SLCA</td>
<td>O</td>
<td>102.0</td>
<td>0.13</td>
<td>3.13</td>
<td>Back-calculated lengths</td>
</tr>
<tr>
<td>PROJMAT</td>
<td>Back</td>
<td>92.0</td>
<td>0.16</td>
<td>3.13</td>
<td></td>
</tr>
<tr>
<td>ELEFAN</td>
<td></td>
<td>265.0</td>
<td>0.13</td>
<td>4.02</td>
<td>This work</td>
</tr>
</tbody>
</table>

S: scales  
O: otoliths  
B: Bhattacharya  
P: Petersen  
Back: back-calculated lengths
DISCUSSION

Of the three length-frequency methods evaluated in the present study, SLCA provided the best values, followed closely by PROJMAT; the results from ELEFAN were clearly inferior to the rest. This was born out in several different analyses: (1) a comparison of growth parameters \( L^\infty \) and \( K \) estimated by the three length-frequency methods with the values resulting from various studies based on counts of growth rings; (2) a comparison of the standard growth index \( \phi^2 \) values derived from the length-based methods and those from studies based on growth rings; (3) the two precision estimates (PE and CV) derived from jackknife iterations; and (4) jackknife simulations involving variations in input data.

Most of the above results are intimately linked to the respective \( L^\infty \) values. A combination of the life cycle characteristics of \( L. \) campechanus, together with the mathematical procedures used by ELEFAN, could explain the consistent overestimation of \( L^\infty \) when using this model. Red snapper populations exhibit multiple recruitment peaks throughout the year (Bradley and Bryan, 1974), and when associated with low \( K \) values, such as seems to be characteristic of this species (Torres et al., 1991), would produce overlapping modes. When analyzed by ELEFAN, these multiple modes result in overestimation of \( L^\infty \). Although one previous study of \( L. \) campechanus (González, 1980) using ELEFAN produced growth parameter estimates comparable to those from other work using growth rings, our results indicate that ELEFAN did not offer reliable results and therefore its use should be abandoned in favor of PROJMAT and SLCA. These two length-based methods can provide as accurate growth estimates as the time-consuming direct methods, and thus their use is recommended to provide growth information more quickly than the traditional analysis of growth rings.

The lowest recommended value for \( K \), when estimating projections from \( t \) to \( t+1 \) in LFDs is 0.5/year (Basson et al., 1988). Hence, it is remarkable that the results of the present study indicate that PROJMAT provides reliable estimates of growth parameters for a long-lived species with \( K \) values well below the recommended minimum. However, this model consistently showed greater variability in precision estimates of growth parameters than those from SLCA. This could be attributed to greater sensitivity in the PROJMAT procedures to the sequential omission of samples. Thus, care should be taken in designing sampling strategies if PROJMAT is to be used in estimating growth parameters.

SLCA consistently provided the best (lowest) CV and PE values, as well as growth parameter estimates within the range reported in the literature, resulting from direct counts of growth rings. This corroborates its usefulness for estimating growth parameters in long-lived species with low growth rates (Basson et al., 1988), such as snappers (Grimes, 1978; Ross and Huntsman, 1982). These findings may be explained by the fact that \( T \) (see Methods) is a continuous function, which although sensitive to modal groups, does not require specifications about the number and position of modes (Sheherd, 1987b; Defeo et al., 1992), and thus gives comparative advantages with regard to ELEFAN and PROJMAT.

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