INTRODUCTION

The Pacific mackerel *Scomber japonicus* is an important commercial fish in the Gulf of California. The species is distributed in the North-eastern Pacific from Alaska to Bahía Banderas (México), and the Gulf of California (Schaefer, 1980). A few studies have examined age and growth of the adult mackerel (i.e. age>1) from California and Baja California using otoliths (Fitch, 1951; Gluyas-Millán and Félix-Uraga, 1990; Gluyas-Millán and Gómez-Muñoz, 1993). However, little is known of the age and growth of larval and juvenile Pacific mackerel. Hunter and Kimberly (1980) described the growth of larvae reared in the laboratory but did not fit growth equations to their data. The larvae and juveniles of several other Scombrids have been aged, including the Bluefin tuna, *Thunnus thynnus* (Brothers et al., 1983), the Yellowfin tuna, *Thunnus albacares*, the Skipjack tuna, *Katsuwonus pelamis* (Uchiyama and Struhsaker, 1981; Radtke, 1983; Yamanaka, 1989), King and Spanish mackerel, *Scomberomorus cavalla* and *S. maculatus* (De Vries et al., 1990), as well as the congeneric Atlantic mackerel, *Scomber scombrus*, from temperate waters (Kendall and Gordon, 1981; Migoya, 1989; D’Amours et al., 1990, and Simard et al., 1992).

The discovery of daily increments in fish otoliths (Pannella, 1971, 1974) has made the interpretation of otolith microstructure a major tool for estimating...
age and growth in larval and juvenile fishes (Campana and Neilson, 1985; Jones, 1986; Stevenson and Campana, 1992). Aging by counting otolith growth increments allows a direct measure of length-at-age for calculation of growth curves and may provide information on individual age and growth rates. Furthermore, back-calculation of daily increments may reveal temporal distribution of birthdates (Methot, 1983). Rates of growth and survival of young fish have also been hypothesized to affect the abundance of the incoming year-classes (Lasker, 1985; Rothchild, 1986). Hence small changes in growth rates can also have a dramatic effect on recruitment by determining the duration of the stage over which high mortality rates may operate (Houde, 1987).

The objectives of our study were to age juvenile (0-year) Pacific mackerel, to model their somatic growth, and to determine their hatching date frequency distribution.

MATERIALS AND METHODS

Juvenile Pacific mackerel (n = 244) were collected between 1990 and 1996 off both the western and eastern shores of the Gulf of California (México) from Bahía Animas to Bahía Yávaros during February, March, May and August (Fig. 1, Table 1). Surface temperatures at collection sites ranged from 21.5 to 28.7°C.

Prior to removing the otoliths, the standard length (SL) was measured to the nearest 0.1 mm. The sagittae were removed and stored dry until mounting. The otoliths were mounted in cyanoacrylate (Krazy Glue™) on a microscope slide. Before examining Pacific mackerel otolith microstructure, we first examined the otolith microstructure of Atlantic mackerel of known age for training purposes.

All observed otoliths were ground with the proximal side facing the slide until the nucleus was reached with self-adhesive 3M Imperial Lapping Film (3 and 30 µm grit). Otoliths were viewed in transmitted light and growth increments counted using a compound microscope. The central part of the otolith (close to the nucleus) was read at 1000x in immersion oil (usually the first 10 to 15 rings), while its outer part (dorso-ventral direction) was examined at 250x magnification (D’Amours et al., 1990). The enumeration of growth increments on the otoliths was made on the shorter axis, according to D’Amours et al. (1990) and Simard et al. (1992). Because the otoliths of mackerel are curved throughout the long axis (rostrum to postrostrum), the increments in the long axis are lost during the grinding. In addition to the number of increments, the otolith diameter in the reading axis was measured. Pacific mackerel display an otolith microstructure similar to the daily increments observed in Atlantic mackerel.

Table 1. – Dates and sampling locations of juvenile Pacific mackerel, Scomber japonicus, from the California Gulf. Standard length in mm and age in days.

<table>
<thead>
<tr>
<th>Date</th>
<th>Region</th>
<th>number of juvenile sampled</th>
<th>number of juvenile aged</th>
<th>Standard Length Interval sampled</th>
<th>Standard Length Interval aged</th>
<th>age range</th>
<th>age average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mar. 1990</td>
<td>Bahía Animas</td>
<td>18</td>
<td>15</td>
<td>45-138</td>
<td>45-135</td>
<td>47-74</td>
<td>62</td>
</tr>
<tr>
<td>May-Aug. 1991</td>
<td>Bahía Guaymas</td>
<td>5</td>
<td>4</td>
<td>90-158</td>
<td>90-158</td>
<td>60-111</td>
<td>87</td>
</tr>
<tr>
<td>May-Aug. 1992</td>
<td>Bahía Animas</td>
<td>11</td>
<td>10</td>
<td>120-162</td>
<td>120-162</td>
<td>50-96</td>
<td>74</td>
</tr>
<tr>
<td>Feb.-May 1993</td>
<td>Bahía Yávaros</td>
<td>21</td>
<td>18</td>
<td>90-146</td>
<td>90-140</td>
<td>44-79</td>
<td>60</td>
</tr>
<tr>
<td>Feb. 1994</td>
<td>Bahía San Rafael</td>
<td>8</td>
<td>8</td>
<td>44-76</td>
<td>44-76</td>
<td>46-54</td>
<td>49</td>
</tr>
<tr>
<td>Feb. 1996</td>
<td>Mulegué</td>
<td>57</td>
<td>50</td>
<td>35-83</td>
<td>35-83</td>
<td>32-53</td>
<td>43</td>
</tr>
</tbody>
</table>

Fig. 1. Study area, Gulf of California.
(Migoya, 1989; D’Amours et al., 1990) as well as in many other fishes [see Stevenson and Campana (1992) for a recent review].

The enumeration of growth increments on the otoliths started from a prominent dark ring near the center present on all otoliths. We postulated that this was a hatch check, based on Migoya (1989), who determined that a similar check on otoliths of reared Atlantic mackerel was a hatch check. We further postulated that the increments were deposited daily, as Migoya (1989) and D’Amours et al. (1990) experimentally determined for Atlantic mackerel. A minimum of three counts was made on all otoliths, and the mean of the counts was used in the analysis. When the three counts differed by more than five rings, the otolith was reread. If there was still disagreement after the second reading, the otolith was not included in this analysis. Ten otoliths were discarded on this basis.

The sagittae of Pacific mackerel juveniles display presumably daily, bipartite growth increments composed of one optically transparent and less transparent layer as well as finer subdaily increments, which were not considered. D’Amours et al. (1990) defined these increments as sharp discontinuous zones and irregular and diffuse rings. They comment that only with the direct validation experiment was it possible to determine that the sharp discontinuous zones were daily, and that the diffuse zones were not to be included in the counts for the estimation of age.

The Gompertz growth curve has previously been found superior to the logistic and the von Bertalanffy curves in describing growth of 0-year Atlantic mackerel (Simard, 1991; Simard et al., 1992). For this reason, early growth in Pacific mackerel was modelled by fitting a Gompertz curve to the length-at-age data using the SYSTAT NONLIN module (Wilkinson, 1987). We used the following formulation of the Gompertz growth equation, according to Ricker (1979, p. 705):

\[ L_t = L_\infty e^{-e^{-g(t-t_0)}} \] (1)

where

- \( L_t \) = standard length (mm) at age \( t \) (days from hatch),
- \( L_\infty \) = asymptotic standard length (mm) at the end of the first growth season,
- \( g \) = instantaneous growth rate when \( t = t_0 \),
- \( t \) = age (days from hatch),
- \( t_0 \) = age of maximal growth (at the inflection point of the curve).

To yield parameter estimates with the smallest variance, a weighting factor equal to the inverse of age was introduced in the least squares analysis, as the variance in length was not homogeneous (Box et al., 1978). This weighting procedure was also used for the same purpose by D’Amours et al. (1990) and Simard et al. (1992). A measure of goodness-of-fit was provided by calculating a coefficient of determination (\( r^2 \)) (Sokal and Rohlf, 1981, p. 673; D’Amours et al., 1990; Simard et al., 1992) and by examining the distribution of residuals.

Following Simard et al. (1992), we assessed interannual variability in growth by comparing growth of fish aged between 32 and 53 days sampled in February 1995 and February 1996 (Table 1). Growth is linear for that age range. Hence we compared linear regressions of length versus age with analysis of covariance (ANCOVA).

The hatching dates frequency distribution of juvenile Pacific mackerel was obtained by subtracting counts of growth increments from the date of capture (Campana and Jones, 1992). This distribution was compared to the spawning season of mackerel in the Gulf of California (Gluyas-Millán and Quiñonez-Velázquez, 1996).

RESULTS

Otolith diameter was highly correlated to standard length for Pacific mackerel juveniles (Fig. 2) \( (r = 0.88, p<0.001, n = 213) \). This highly significant relationship demonstrates that fish growth and otolith
growth are closely coupled. This observation is consistent with the hypothesis that the increments are formed daily. As additional validation we compared our age estimations with the age and length data of Hunter and Kimbrell (1980), in the interval of 26 to 47 days of age. The slope of Hunter and Krimbrell’s data, when plotted against the regression line of the present study (Fig. 3), shows close agreement (ANCOVA, \( p = 0.986, n = 9 \)). This comparison suggests that growth increments are deposited daily and that growth of reared and wild fish is similar.

A total of 244 juvenile Pacific mackerel was available from seven sampling programs (Table 1). Fish ranged in size from 31 to 162 mm SL, and in age from 27 to 111 days. Juvenile distribution varied

![Fig. 3. – Comparison between the ages estimated from otoliths and laboratory reared juvenile Pacific mackerel, *Scomber japonicus*. The vertical bars represent standard deviation.](image)

![Fig. 4. – Size and age distribution of juvenile Pacific mackerel, *Scomber japonicus*, collected between 1990 and 1996.](image)
by size and age. The smaller fish were generally caught early in the year (February to May) (Fig. 4) and farther south from Bahía de Guaymas, whereas larger individuals were taken later in the year (May-August) from locations farther north (Bahía Animas). Younger fish were collected only from February to May, whereas older fish were collected only from May to August (Fig. 4).

Back-calculated hatching date frequency distribution of juveniles (Fig. 5) showed that spawning occurs over a long period, from October to May, but it is concentrated mostly in December, January, and February. This is in agreement with the observation that female Pacific mackerel ovaries are usually ripe from December to February in the Gulf of California (Gluyas-Millán and Quiñonez-Velázquez, 1996).

Age length data of the juvenile Pacific mackerel (data of all years combined) were well described by a Gompertz equation ($r^2 = 0.85$) (Fig. 6):

$$L_t = 187.36 e^{-0.35(t-43.92)}$$

Projecting the Gompertz growth curve to ages younger than 27 days, it is observed that the projected region of the curve was biologically reasonable and coincided well with the length age data of the laboratory reared Pacific mackerel by Hunter and Kimbrell (1980). Growth in length of Pacific mackerel juveniles was rapid after metamorphosis until 50 days after hatching. The maximum daily growth rate was 1.91 mm d$^{-1}$ between the ages of 44

<table>
<thead>
<tr>
<th>Age (days)</th>
<th>Growth rate (mm d$^{-1}$)</th>
</tr>
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<tbody>
<tr>
<td>25-30</td>
<td>1.59</td>
</tr>
<tr>
<td>30-35</td>
<td>1.76</td>
</tr>
<tr>
<td>35-40</td>
<td>1.87</td>
</tr>
<tr>
<td>40-45</td>
<td>1.91</td>
</tr>
<tr>
<td>45-50</td>
<td>1.90</td>
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<tr>
<td>50-55</td>
<td>1.83</td>
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<td>55-60</td>
<td>1.73</td>
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<td>60-65</td>
<td>1.60</td>
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<td>65-70</td>
<td>1.46</td>
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<tr>
<td>70-75</td>
<td>1.32</td>
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<tr>
<td>75-80</td>
<td>1.17</td>
</tr>
<tr>
<td>80-85</td>
<td>1.04</td>
</tr>
<tr>
<td>85-90</td>
<td>0.91</td>
</tr>
<tr>
<td>90-95</td>
<td>0.79</td>
</tr>
<tr>
<td>95-100</td>
<td>0.68</td>
</tr>
<tr>
<td>100-105</td>
<td>0.59</td>
</tr>
<tr>
<td>105-110</td>
<td>0.51</td>
</tr>
</tbody>
</table>

Table 2. – Predicted absolute growth rates (mm d$^{-1}$) of Pacific mackerel, *Scomber japonicus*, for five day intervals between the ages of 25 and 110 days in the California Gulf.

![Fig. 5. – Back-calculated hatch time of juvenile Pacific mackerel, *Scomber japonicus*, from the Gulf of California.](image)

![Fig. 6. – Gompertz growth curve fitted to length and age data for Pacific mackerel, *Scomber japonicus*. The thin portion of the Gompertz growth curve represents the projected region.](image)
and 45 days, while the mean growth rate for ages between 50 to 110 days of life was 1.13 mm d⁻¹ (Table 2). This growth curve is based on length-at-age data from 204 specimens with a 31-162 mm SL range and a 27-111 days age range.

Finally, we did not detect interannual growth variability between juveniles sampled in February 1995 and February 1996 (ANCOVA, p = 0.683, n = 142).

DISCUSSION

Distinct growth increments were visible on the sagittae of Pacific mackerel juveniles, which we assumed to have been deposited daily. Considering that most if not all species in which periodicity of growth increments has been determined (including several Scombrids) were found to deposit one increment per day (see reviews by Campana and Neilson, 1985, Jones, 1986, and Stevenson and Campana, 1992), we believe this assumption to be correct. Cases where deposition rates appeared to have been non-daily appear to be artifacts caused by lack of resolving power of light microscopy in slow growing fish (Campana and Neilson 1985). We also assumed that increment formation started at hatching. Initial increment formation may occur before hatching, at hatching, or at the onset of exogenous feeding (Brothers et al., 1976; Lough et al., 1982). Migoya (1989) reported that Atlantic mackerel initiated ring formation at hatching. Laboratory studies are needed to determine the age of formation of the first increment and to validate the daily periodicity of increment formation in Pacific mackerel.

The Gompertz growth curve adequately fits the length-at-age data for juveniles but may have underestimated the length of larvae. The growth equation predicts that 2-day-old larvae are 2.6 mm SL while Hunter and Kimbrell (1980) reported that larvae reared in the laboratory at 22.1°C were 3.3 ± 0.21 mm long (SL ± SD). This value is 27% larger than the length predicted by the model. Moreover, the model predicts that 19-day-old larvae are 17.6 mm SL whereas 19-day-old reared larvae had a mean SL of 24.1 mm (Hunter and Kimbrell, 1980).

Grouping data from different years was done to cover the age range as much as possible, but this grouping may have biased resulting growth patterns. However, we argue that such bias must have been minimal since juveniles sampled in February of 1995 and 1996 grew at a similar rate. Fig. 4 also suggests that growth variations are not important for fish collected at similar dates. Size-selective mortality of juveniles may also have biased the growth pattern, but this is unknown.

The higher water temperatures experienced by early stages of Pacific mackerel [(e.g. 21-26°C in the Gulf of California (Gluyas-Millán, 1989)] compared to those of Atlantic mackerel [8-18°C (Sette, 1943)] are not translated into a higher daily growth rate in the former but rather into a lower mean growth rate. We found that up to 110 days old, Pacific mackerel grew on average 1.33 mm d⁻¹ whereas up to 90 days old, Atlantic mackerel exhibited a mean growth rate of 1.95 mm d⁻¹ (Simard et al., 1992). Despite this, the maximal body lengths reached by the end of first growing season (the L∞ of the Gompertz equation) are about the same for both species indicating that the growing season of Pacific mackerel is probably longer than in that of Atlantic mackerel. It should be noted, however, that neither this study nor Simard et al. (1992) had age data in the L∞ area of the curve to validate the Gompertz L∞ values. One effect of higher water temperatures on early life history of Pacific mackerel versus Atlantic mackerel concerns the incubation period. Eggs of Pacific mackerel have incubation times ranging from 1.3 days at 23°C to 4.8 days at 14°C (Hunter and Kimbrell, 1980). By comparison, Atlantic mackerel eggs reared at 10°C, 14°C, and 20°C hatched after incubating for 8.7, 4.6, and 2.4 days, respectively (Worley, 1933).

The wide distribution of hatching dates of juveniles reflects the protracted spawning period. This observation is corroborated with the monthly distribution of mature females (Gluyas-Millán and Quiñonez-Velázquez, 1996). This species spawns at various times of the year; in addition, each female spawns several egg batches (Dickerson et al., 1992). As a result, newly hatched larvae experience a wide range of environmental conditions that can induce variability in growth rates and survival during the first year of life.

In conclusion, we have described and modelled for the first time daily growth of juvenile Pacific mackerel under explicit and well-grounded assumptions on periodicity of increment formation. We have also compared juvenile growth features between Pacific mackerel and Atlantic mackerel.

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