

**Abstract.**—Pacific red snapper, *Lutjanus peru*, collected from commercial hook-and-line gear and shrimp trawls off the southeast coast of Baja California Sur, Mexico, were aged by using scales and otoliths (whole-otolith and sectioned-otolith readings). Comparison of ages determined from these structures revealed that scales tend to underestimate ages beyond 5 years, often by more than 1 year, and that they are the least precise structures for aging. Sectioned otoliths gave greater estimates of age than whole-otolith counts (mean differences <1 yr) and were the most precise structure. The von Bertalanffy growth function described *L. peru* growth satisfactorily with length-at-age determined from whole otoliths and sectioned otoliths. Parameters for the entire population were  $L_{\infty} = 97.32$  cm,  $K = 0.1111/\text{yr}$ ,  $t_0 = -0.316$  yr ( $n=1180$ ). No significant differences in length-at-age were found between sexes. The largest individual was a 31-year-old 99.2-cm-TL male, constituting a maximum age, and length record for this species. A multiple regression model of whole-otolith age as a function of otolith and fish measurements provided satisfactory results. Total mortality rates were significantly lower for females ( $Z=0.282/\text{yr}$ ) than for males ( $Z=0.366/\text{yr}$ ).

## Age, growth, mortality, and population characteristics of the Pacific red snapper, *Lutjanus peru*, off the southeast coast of Baja California, Mexico

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The Pacific red snapper, *Lutjanus peru* (Nichols and Murphy), known as "huachinango" in Mexico, is distributed throughout the lower Gulf of California to Peru and found in offshore schools over rocky bottoms to depths exceeding 100 m. It is a commercially important species in Mexico as well as in Central and South America (Thomson et al., 1987; Gutiérrez Vargas, 1990; Ramírez Rodríguez and Rodríguez Medrano, 1990).

*Lutjanus peru* is fished in most Mexican states along the Pacific coast. The highly valued product is generally marketed whole and transported to inland cities, or occasionally exported. Nationwide, it shares a market with its congener, the Gulf of Mexico red snapper *Lutjanus campechanus* Poey. From 1980 to 1988, the reported catches of both species averaged 6556 metric tons (t) per year (SD 1290 t/yr), of which 56% originated in the Pacific.<sup>1</sup> In Baja California Sur, Pacific red snapper is fished on a small artisanal scale; near Cerralvo Island, *L. peru* ranks within the six most important exploited finfishes (Fig. 1) (Ramírez Rodríguez and Rodríguez Medrano, 1990). As is the case with other snappers, juveniles

of this species aggregate over soft bottoms where they are caught as bycatch during shrimp trawling activities (Van Der Heiden, 1985; author's personal observations).

Information on the biology of *L. peru* is limited despite its ecological and commercial importance. Gorelova (1979) performed feeding experiments on juvenile *L. peru* caught off the coast of Peru, whereas Ruiz Santos (1983) studied the reproductive biology of the species off the southwest coast of Mexico and Ruiz and Madrid (1992) studied the biology of a parasitic isopod and its effects on *L. peru* hosts off Michoacán. With the exception of Rocha Olivares and Gómez Muñoz (1993), age and growth of the Pacific red snapper have been estimated either from scales in Mexico (Castro, 1981; Ruiz Luna et al., 1985; Aguilar Salazar, 1986) or from length-frequency distributions in Costa Rica (Gutiérrez Vargas, 1990). The use of scales, however, may result in less than accurate age estimates for some

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species, including systematic underestimations (e.g. Bilton, 1973; O'Gorman et al., 1987; see review by Beamish and McFarlane, 1987, and papers therein).

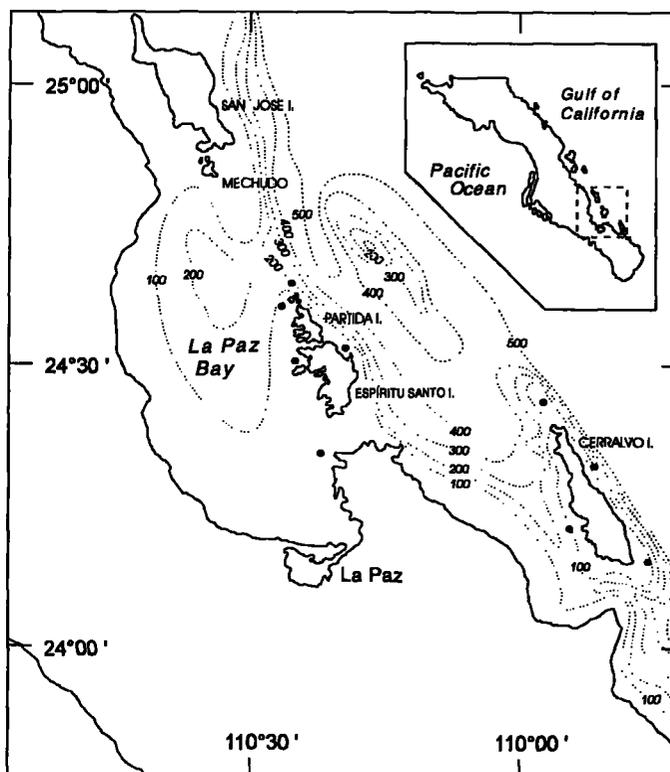
Because of the lack of reliable information on biological parameters for this commercially important tropical species, this work represents the first comprehensive study of growth and mortality of a *L. peru* population based on otolith age determinations. A comparison of age estimates from whole and sectioned otoliths and from scales is made to assess their relative usefulness. Growth and mortality rates are estimated, and other aspects of the biology are presented for an exploited population of the Pacific red snapper off the southeast coast of Baja California Sur.

## Materials and methods

### Study area and sampling scheme

This study took place in Bahía de La Paz, one of two major bays in the Gulf of California (Walker, 1960). The most important fishing grounds for *L. peru* lie within and southeast of the Bay, around Espíritu Santo-Partida and Cerralvo Islands (Fig. 1). Peak catches occur during the summer.

Pacific red snapper were collected from March 1989 to March 1991. Most samples came from La Paz City fish market, which was sampled at least weekly, March 1989 to February 1991. Snappers were also collected monthly with baited hook and line, May 1989 to February 1991. Juvenile red snappers were collected as shrimp trawler bycatch during February and March 1991. Biological samples were taken from all fish collected ( $n=2605$ ). In the market, sampling time was limited to the period before fish were stored, therefore biological sampling was restricted to the first 20 randomly selected individuals from each 4-cm length interval. Biological samples consisted of both sagittae, at least 10 scales from underneath the left pectoral fin, and testes and ovaries, which were fixed in 10% buffered formalin and used for sex determination and reproduction studies. Total and standard lengths (TL and SL, respectively) were measured to the nearest mm; total and gutted weights (TW and GW, respectively) were recorded to the nearest 2 or 5 g, depending on fish size. Since fish were gutted on landing, some data and samples could not be obtained from the market. However, many gutted fishes could be sexed from gonadal remains. In 1989, when samples were most abundant,



**Figure 1**

Map of study area showing approximate positions (•) of fishing grounds and sampling sites of Pacific red snapper *Lutjanus peru*. Depth contours are in fathoms.

3085 additional fishes were measured to construct sex-specific length-frequency distributions.

### Sample processing and age determination

Because the left and right sagittae did not differ morphometrically<sup>2</sup> or in weight (paired *t*-tests,  $P>0.5$ ) in a random subsample of 50 fishes representative of the length range available and since no differences were found in their marking pattern or number of rings, the right otolith was used for age determination when available. Otoliths were submerged in 90% glycerol for 24 hours before they were viewed under a dissecting scope with reflected light over a darkened background. Otoliths embedded in thermoplastic cement were sectioned with a low-speed saw. Three sections (0.3 mm thick), including the primordium and the flanking regions, were made orthogonal to the anteroposterior axis of the structure. Sections were glued to glass slides with cyanoacrylate-based cement and prepared for observation as de-

<sup>2</sup> Measurements compared are those described in Rocha Olivares and Gomez Muñoz (1993).

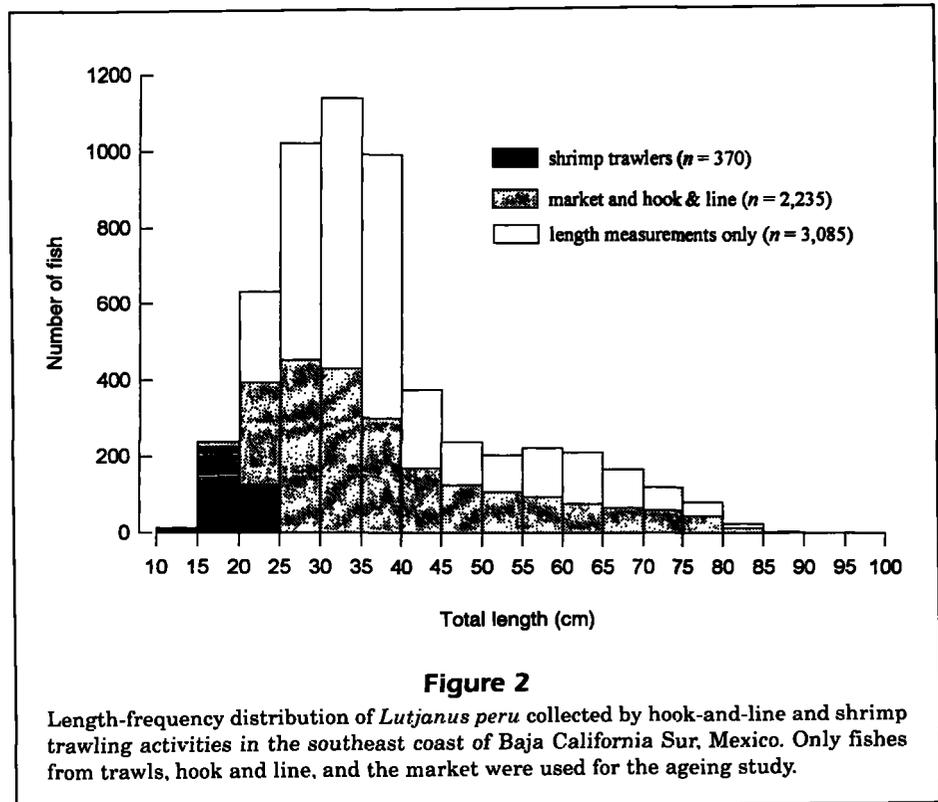
scribed for whole otoliths. Scales were mounted intact between two glass slides and observed under a dissecting microscope at different magnifications with transmitted light.

Organisms were aged by counting the number of growth marks found in scales (scale age), whole otoliths (whole-otolith age), and sectioned otoliths (sectioned-otolith age). Because a large number of fishes occurred within a restricted length range (Fig. 2), age estimates for whole-otolith ring counts were made on 50 randomly subsampled otoliths from each 2-cm fish-length interval ( $n=1356$ ) (FAO, 1982). After whole-otolith age determinations were made, a stratified random subsample of these otoliths was sectioned ( $n=151$ ) and the corresponding scales were used for ageing (10 per fish). Only nonregenerated scales were used for age determinations.

Two independent whole-otolith age determinations were made at different times by two readers. A third estimate was then made three months later for those otoliths with different ages. Lack of consensus resulted in the otolith being discarded as "noninterpretable," and excluded from the growth analysis. An effort was made to note the cause for rejection. Sectioned otoliths and scales were subject to two reading rounds by one reader separated by a three-month interval.

Estimates of the precision (variation between different reading rounds for each structure) and of the corroboration (variation among structures) were assessed by comparing the percentage of discordant determinations between two data sets (%D) and the index of average percent error of Beamish and Fournier (%E) (1981).

Following the method proposed by Boehlert (1985) of using objective criteria and multiple regression models to determine fish age from otolith measurable parameters, an effort was made to predict Pacific red snapper whole-otolith age by using otoliths and fish morphometrics. This method, originally conceived to save time and costs as well as to reduce the subjectivity involved in otolith reading, was implemented on *L. peru* data and the resulting model used to determine the age of fishes whose otoliths could



not be read. Independent variables included otolith weight (to the nearest mg), width, length, ventral radius, anterior radius, fish TL, GW, their logarithmic transformations and squared terms, and a modified condition factor  $K$  (gutted weight/  $TL^3$ ). Data from a stratified random subsample (FAO, 1982) from the whole-otolith age determinations were used for this analysis ( $n=285$ ). A stepwise procedure with an inclusion level of  $P=0.05$  was used to select variables for the model. Homoscedasticity and normality were evaluated by residual analysis (Zar, 1984).

### Growth

Individual length-at-age (whole-otolith and sectioned-otolith) data were used to fit the von Bertalanffy growth function (VBGF):

$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

where  $L_t$  = length at age  $t$ ;  
 $L_\infty$  = asymptotic length;  
 $K$  = growth coefficient; and  
 $t_0$  = age at which fish length would be zero if it grows according to the model.

Hotelling's  $T^2$  test (Bernard, 1981) was used to compare growth parameters.

Observed length-at-age data were obtained from whole-otolith readings for most fishes ( $n=1170$ ) and from sectioned-otolith readings for the largest specimens ( $n=10$ ). To correct for within-year growth, ages were assigned as follows. Since translucent margin deposition on the otolith peaks in July (Rocha Olivares and Gomez Muñoz, 1993; Fig. 3), only fishes caught during this month were assigned integer ages. For the rest, subsequent growth was accounted for by assigning fractional ages in proportion to the elapsed time (e.g. a fish with two annuli caught in January was assigned 2.5 years).

Length-weight relationships were fitted to the data and used to calculate the von Bertalanffy asymptotic weight ( $W_{\infty}$ ). Growth performance  $\phi = \log_{10}(K) + 2/3 \log_{10}(W_{\infty})$  was computed from the growth parameters (Manooch, 1987).

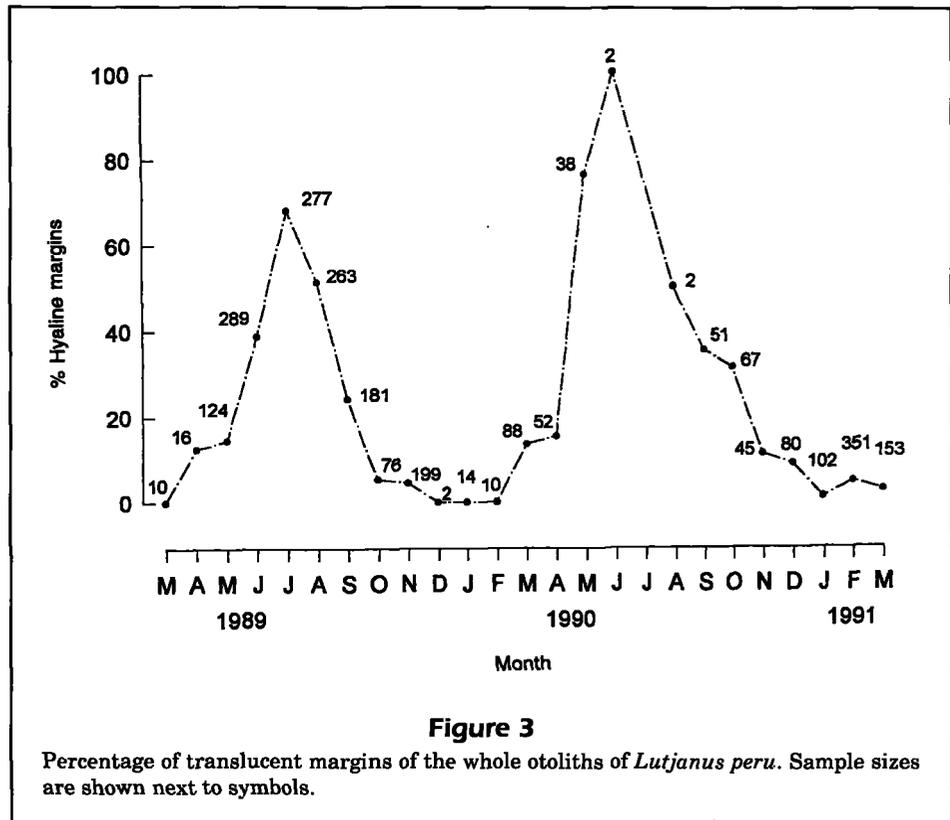
All coefficients of determination reported for non-linear models were computed by using the following expression (Draper and Smith, 1981):

$$R^2 = 1 - \frac{\sum (y - \hat{y})^2}{\sum (y - \bar{y})^2},$$

where  $y$  = observed values;  
 $\hat{y}$  = predicted values; and  
 $\bar{y}$  = mean values.

### Mortality

An age-length key was constructed from whole-otolith ages for the sexes combined and applied to the length-frequency distributions to construct population age distributions by sex. Total mortality rate ( $Z$ ) was determined from the descending limb of the resulting catch curves for males, females, and pooled sexes. Hoenig's (1983) combined regression equation was used to obtain another estimate of  $Z$ . Owing to the lack of data concerning fishing effort and the unavailability of unfished areas, no direct estimation of the natural mortality rate ( $M$ ) was possible. Instead, empirical relationships between  $M$  and  $K$



**Figure 3**  
 Percentage of translucent margins of the whole otoliths of *Lutjanus peru*. Sample sizes are shown next to symbols.

were used to obtain approximate estimates (Pauly, 1980; Ralston, 1987). A mean bottom temperature of 14°C was assumed for calculating  $M$ . This temperature prevails throughout most of the Gulf at depths between 100 and 300 m (Maluf, 1983).

### Results

#### Population parameters and morphometric relations

During the sampling period *L. peru* abundance was variable, and in some months (e.g. March and December 1989 and July to August 1990), sample size was small because of limited supply. Sex determination was possible for only 13.1% of the specimens used for length-frequency distributions (males:females=1:0.84;  $H_0=1:1$  ratio,  $\chi^2_c=2.85$ ,  $P=0.091$ ). In the biological sampling, the sex ratio was 1:0.85 ( $H_0=1:1$  ratio,  $\chi^2_c=5.36$ ,  $P=0.021$ ), indicating that no bias was introduced in the length-frequency sampling with only gonad fragments.

Macroscopic gonad differentiation occurs in *L. peru* between 30 and 35 cm TL (Table 1). A significant fraction of the catch included individuals smaller than 50 cm TL (38% of a total of 2171 kg of gutted fish).

**Table 1**

Total length composition (cm) of the biological sample of Pacific red snapper by sex. The column labeled "unsexed" groups fishes with undifferentiated gonads (almost all of those <30 cm) and those gutted and with no traces of gonadal tissue (most of those between 30 and 40 cm and all of those > 40 cm).

Size range	Males	Females	Unsexed	Total
10.1-15.0	0	0	24	24
15.1-20.0	0	0	259	259
20.1-25.0	4	5	366	375
25.1-30.0	23	23	404	450
30.1-35.0	67	59	305	431
35.1-40.0	109	76	117	302
40.1-45.0	66	46	59	171
45.1-50.0	40	28	56	124
50.1-55.0	32	24	52	108
55.1-60.0	37	17	38	92
60.1-65.0	26	25	26	77
65.1-70.0	26	23	18	67
70.1-75.0	21	29	11	61
75.1-80.0	9	30	7	46
80.1-85.0	5	9	0	14
85.1-90.0	0	3	0	3
90.1-95.0	0	0	0	0
95.1-100.0	1	0	0	1
Total	466	397	1742	2605

Male and female length compositions were significantly different (Kolmogorov-Smirnov two-sample test,  $D=0.0836$ ,  $0.01 < P < 0.05$ ). Although the largest specimen was a 99.2-cm-TL male (Table 1), females predominated beyond 70 cm (sex ratio 1:1.97).

Conversion equations for lengths (cm) and weights (kg) did not differ between sexes (ANCOVA,  $P > 0.05$ ); therefore data were pooled:

$$TL = 1.246SL + 0.104 \quad (n=2603, r^2=0.997, P<0.001)$$

$$TW = 1.207GW - 0.020 \quad (n=841, r^2=0.988, P<0.001)$$

$$GW = 1.763 \times 10^{-5} TL^{2.877} \quad (n=2350, R^2=0.990, P<0.001)$$

$$TW = 1.816 \times 10^{-5} TL^{2.905} \quad (n=844, R^2=0.980, P<0.001)$$

Exponents of the length-weight relationships were significantly different from three ( $t$ -test,  $P < 0.05$ ).

### Age determination

Concentric annuli and circuli were observed in most otoliths and scales. Most scales were found to be interpretable, although circuli were never as clearly defined as otolith annuli. Most samples ( $n=92$ ) pre-

**Table 2**

Values of percent disagreement (%D) and percent average error (%E) for whole-otolith, sectioned-otolith, and scale age determinations for individual structures (precision) and between the structure and whole-otolith age (between structures) of Pacific red snapper. No. = number of determinations. Rejections are otoliths not included in the analysis for being too large (size) or for lacking a clear marking pattern (other).

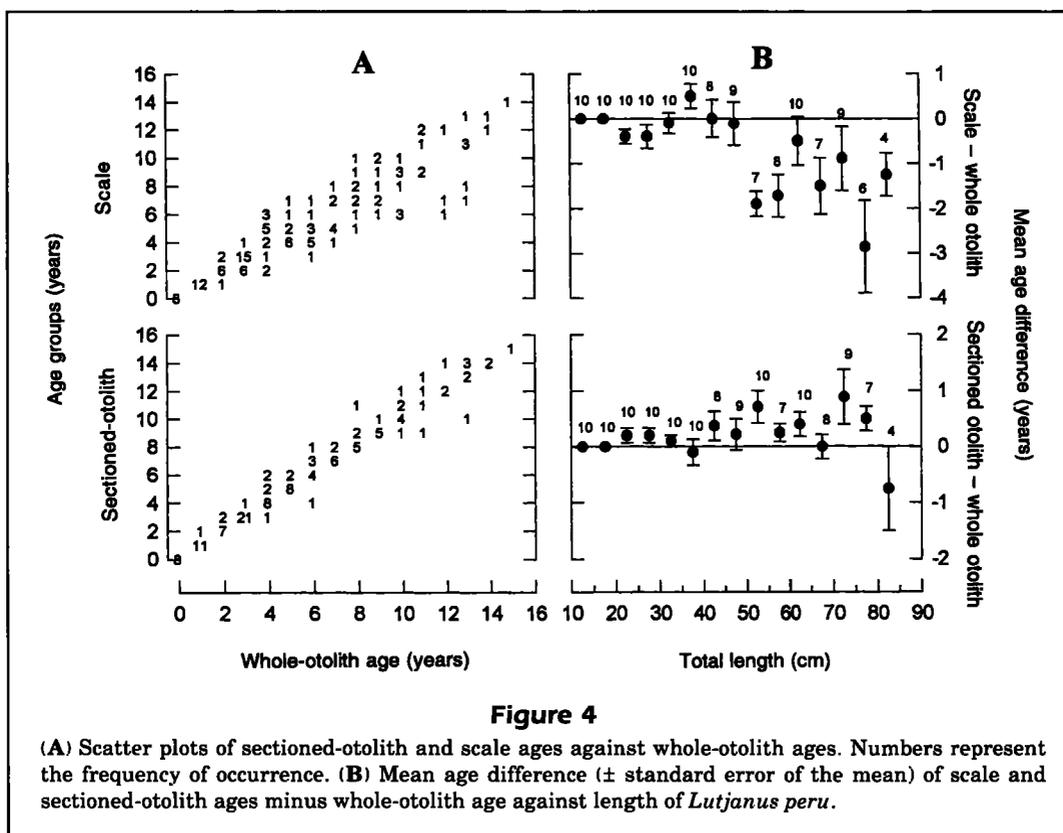
Age	Index		Rejections		
	%D	%E	No.	Size	Other
<b>Precision</b>					
Whole-otolith	16.90	3.89	143	7	1
Sectioned-otolith	10.42	2.13	144	1	6
Scale	34.01	4.19	147	2	2
<b>Between structures</b>					
Sectioned-otolith	26.36	2.82	129		
Scale	58.65	8.86	133		

sented less than 40% regenerated scales. A correlation was found between the percentage of regenerated scales and fish length ( $r=0.310$ ,  $P < 0.001$ ).

Of the 1356 otoliths used for whole-otolith age determinations, 186 were discarded for the following reasons: large size prevented the enumeration of all the growth rings (2.2%), breakage or loss (1.4%), deformities or abnormal calcification (2.3%), and noninterpretable otoliths as defined in the "Methods" section (7.8%). Whole-otolith ages were available for 1170 individuals ranging from 10.2 to 83.5 cm TL.

A number of scales and otoliths were also rejected in the comparison of whole-otolith, sectioned-otolith, and scale ages (Table 2). Noninterpretable otoliths were included in the computation of precision indices, but not in the between-structures indices. Most of the rejections of whole otoliths were due to size, but a similar proportion of sectioned otoliths lacked a clear marking pattern. Sectioned otoliths and scales were the most and least precise structures, respectively, for age determination (Table 2). The %D indicates a factor of three difference in the precision of sectioned otoliths and scales. However, the %E shows that such differences are less important (less than a factor of two) because this index incorporates the difference in age estimations (Beamish and Fournier, 1981). The difference between whole-otolith ages and sectioned-otolith or scale ages was much larger (Fig. 4). Sectioned-otolith ages were found to be at least twice as similar to whole-otolith ages as scale ages according to %D, and more than three times as similar according to %E (Table 2).

The magnitude of the discrepancies in age determinations among structures increased with both age and length of the fish (Fig. 4). Differences between scale



and whole-otolith ages were as large as six years, whereas for sectioned otoliths, differences did not exceed three years (Fig. 4A). Scale ages were consistently lower than whole-otolith ages in fish larger than 50 cm TL, whereas the largest sectioned-otolith and whole-otolith age deviations were found in fish above 40 cm TL (Fig. 4B). The mean sectioned-otolith and whole-otolith age deviations did not exceed one year, although mean scale and whole-otolith age deviations often exceeded one year.

Six independent variables with highly significant coefficients were included in the multiple regression model (Table 3). The model explained 96% of the variability in the data with a standard error of less than one year. A linear regression of whole-otolith age on otolith weight alone accounted for 93% of the variance. The residuals revealed a trend indicating a certain degree of heteroscedasticity but were normally distributed ( $\chi^2=10.41, P=0.005$ ). Whole-otolith ages determined with the multiple regression model for 28 fish with unreadable otoliths were very close to the VBGF (see "Discussion" section).

### Growth

Mean observed length-at-age were not significantly different between sexes, (*t*-tests,  $0.95 > P > 0.09$ ), however

**Table 3**

Regression coefficients for the multiple regression model of whole-otolith age as a function of otolith and fish measurements of Pacific red snapper. SE = coefficient standard error, SEE = standard error of the estimate. *R* = multiple correlation coefficient; No. = number of observations.

Variable	Coefficients	SE	<i>P</i>
Intercept (c)	-6.183	1.0940	0.000
Total length squared	1.306E-03	1.4910E-04	0.000
ln(Gutted weight)	1.353E-05	3.1700E-06	0.000
Otolith weight squared	5.915	0.7313	0.000
Otolith width squared	-7.391E-01	2.4400E-01	0.000
ln (otolith ventral radius)	2.153E-02	7.6050E-03	0.005
Otolith weight	-1.014E-02	3.3360E-03	0.003
		<i>R</i> =	0.9797
		SEE =	0.6469
		No. =	283

male and female VBGF parameters computed separately from individual data were significantly different ( $T^2=609.5, P < 0.001$ ) (Fig. 5). The 99% Roy-Bose simultaneous confidence intervals indicated that the three VBGF parameters significantly contributed to the observed difference in predicted growth ( $6.091 \leq L_{\infty}$

(male)  $-L_{\infty}$ (female)  $\leq 8.419$ ,  $-0.026 \leq K(\text{male}) - K(\text{female}) \leq -0.020$ ,  $-0.511 \leq t_0(\text{male}) - t_0(\text{female}) \leq -0.344$ .

Of the thirty otoliths too large for whole-otolith reading, ten were randomly selected, sectioned, and read, yielding ages of 15 years and above. The VBGF parameters computed from all available data, including whole-otolith and sectioned-otolith ages ( $n=1180$ ) were considered to be representative of the population (asymptotic standard error):  $L_{\infty} = 97.32$  cm (1.816),  $K = 0.1111/\text{yr}$  ( $4.073 \times 10^{-3}$ ),  $t_0 = -0.316$  (0.0569) ( $n=1180$ ,  $R^2=0.93$ ). The asymptotic length was converted to an asymptotic weight of  $W_{\infty} = 10.84$  kg. The growth performance of *L. peru* was  $\phi = 1.736$ . The age composition of the sampled males differed significantly from that of the females (Kolmogorov-Smirnov two-sample test,  $D=0.0843$ ,  $0.01 < P < 0.05$ ) (Fig. 6).

## Mortality

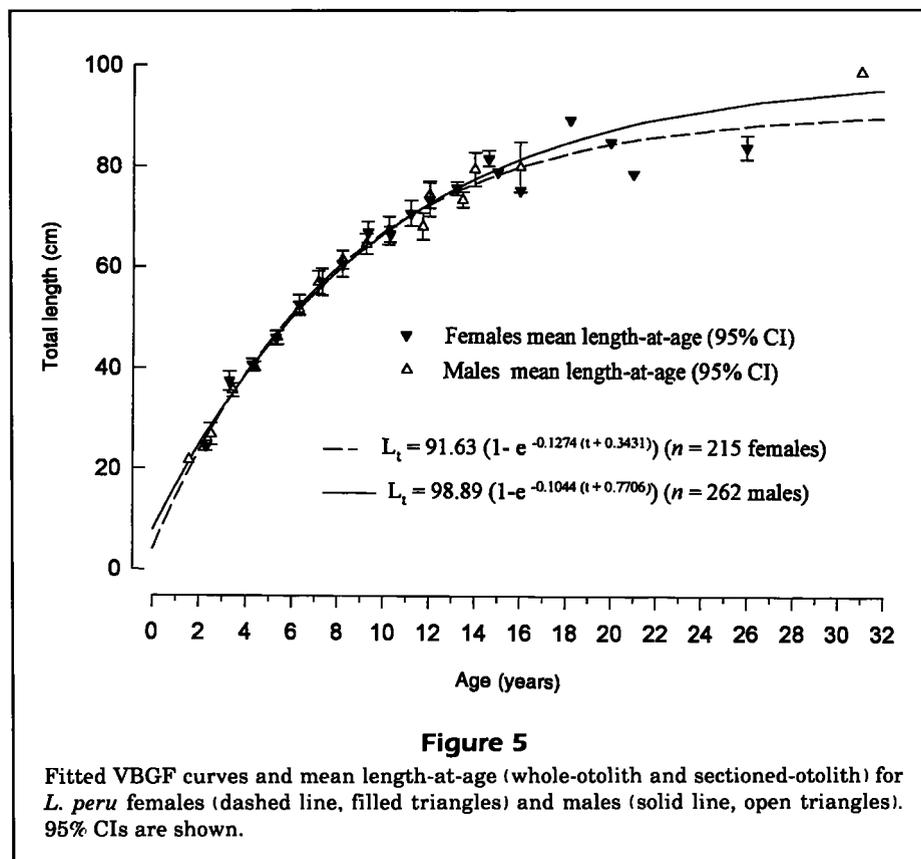
The length range of most age groups was on the order of 20 cm (Table 4: Fig. 7A). Catch curves were constructed for males, females, and pooled sexes. Total mortality rates ( $Z$ ) were calculated without the extreme age groups and those not fully recruited to the fishery (Fig. 8). Total instantaneous mortality

rate for females, estimated from the catch curves, was significantly lower compared with those for males ( $t=-2.112$ ,  $df=52$ ,  $P < 0.001$ ). Hoenig's formula should be applied to the maximum age of "the largest few fish" (Hoenig, 1983). On the basis of this recommendation and the fact that only one out of 5690 fishes measured in this study was larger than 90 cm, this 31-year-old fish was interpreted as an outlier and a  $t_{max} = 26$  years was considered more representative of the population. This value yielded a  $Z = 0.172/\text{yr}$ , which is considerably lower than the catch curve estimates. The estimates of  $M$  obtained from the empirical relationships  $0.222/\text{yr}$  (Pauly, 1980) and  $0.248/\text{yr}$  (Ralston, 1987) were compatible with the catch curve mortality estimates giving exploitation rates  $F/Z$  ranging from 0.121 (females) to 0.393 (males).

## Discussion

### Sampled length range

The accurate estimation of growth parameters depends, among other factors, on the adequate sampling of the length range of a species. The fish used in this study covered most of the known length range of the Pacific

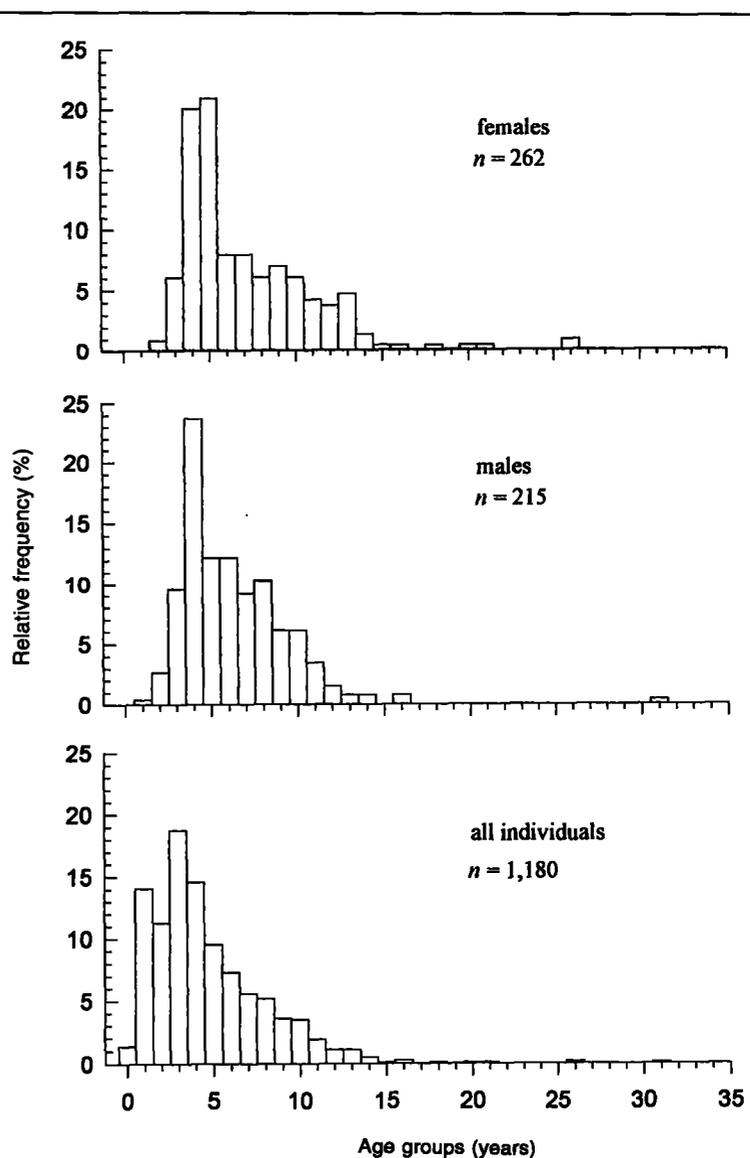


red snapper (10 to ca. 100 cm TL). The lower size limit of *L. peru* in the hook-and-line catch (18.3 cm) was very close to that reported for *L. campechanus* fished with similar size hooks in the Gulf of Mexico (18.0 cm) (Nelson and Manooch, 1982). This might indicate a comparable vulnerability due to morphological similarity. Because fishermen do not typically change hook size to target small snappers (personal observation), the preponderance of small fish in the catch (ca. 61% in numbers) that had not yet recruited to the spawning population was not due to gear selectivity. The upper limit of the range was also sampled and a length record is reported for the species. Thus it seems unlikely that the growth parameters of *L. peru* may be biased owing to inadequate sampling of its length-range.

### Age determination

The monthly fluctuation in the percentage of translucent margins suggests that the period of translucent ring formation takes place in the summer during the spawning season (Fig. 3). This observation enabled Rocha Olivares and Gómez Muñoz (1993) to indirectly validate whole-otolith rings as annuli in *L. peru* up to 10 years old.

The greater precision of sectioned otoliths suggested by %D and %E resulted from a more direct access to the marking patterns of the structure. Different degrees of wear and tear were noted on the anterior margin of large scales, which contributed to age determination variability within reading rounds. Comparison of individual age estimates of *L. peru* from whole otoliths, sectioned otoliths, and scales provided evidence supporting age underestimation by the latter. This underestimation by scales has also been observed in the Antarctic fish *Notothenia gibberifrons* Lonnberg (Coggan et al., 1990). Libby (1985) also concluded that whole-otolith ages were more accurate and less subjective than scales for ageing the anadromous alewife, *Alosa pseudoharengus* (Wilson). As in other species, however, this effect does not seem to be very important during the first five years in *L. peru*. For example, Lou (1992) found that either scales or sectioned otoliths provided reliable age es-



**Figure 6**

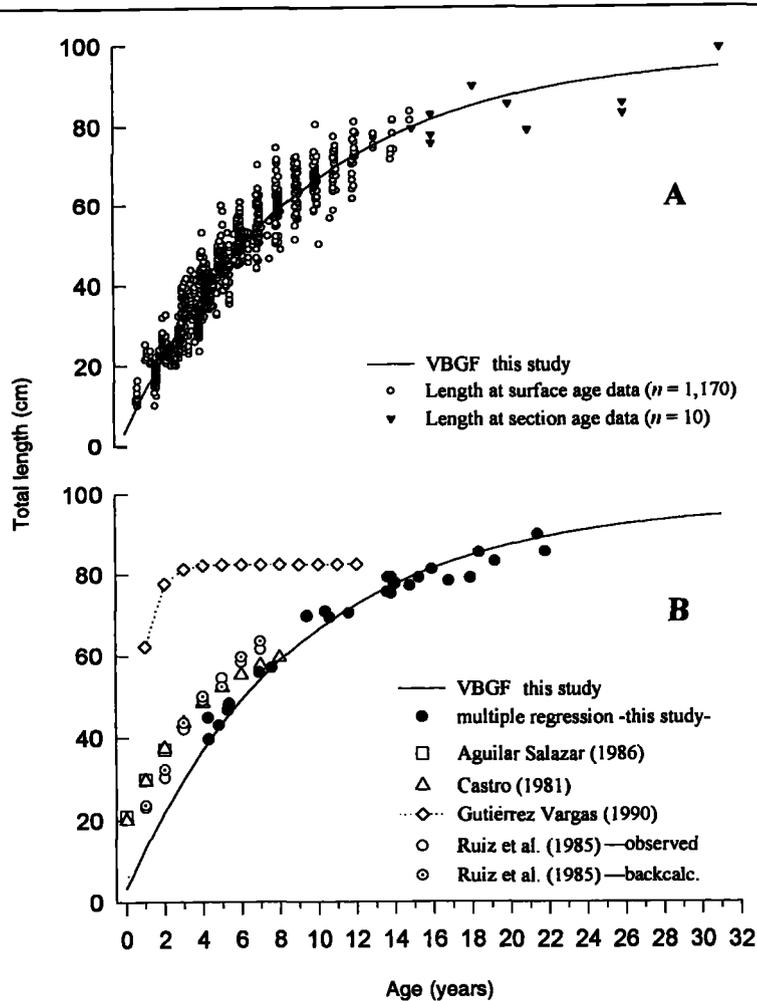
Age structure of *Lutjanus peru* females, males, and sexes combined of directly aged specimens collected at La Paz fish market or caught by hook-and-line and shrimp trawling activities off the southeast coast of Baja California Sur. Data represent whole-otolith ages (up to 15 years) and sectioned-otolith ages (beyond 15 years). Most of the unsexed individuals are undifferentiated fish but some are reproductively active adults that could not be sexed.

timates up to five years in the tropical parrotfish *Scarus schlegeli* (Bleeker), and Lowerre-Barbieri et al. (1994) reported similar findings in weakfish, *Cynoscion regalis* (Bloch and Schneider), to age six. Apparently, otoliths are more reliable structures than scales (Beamish and McFarlane, 1987) over most ages, and this study extends this observation to the Pacific red snapper.

A number of studies have compared whole and sectioned otoliths as alternative structures for age determination. The magnitude of the difference between whole-otolith and sectioned-otolith age varies from species to species, but the general trend is an underestimation of whole-otolith ages in older fishes. Wilson and Boehlert (1990) found that sectioned-otolith ages produced smaller  $L_{\infty}$  estimates than whole-otolith ages, but growth rates were similar for both in the canary rockfish, *Sebastes pinniger* (Gill).

In the long-lived orange roughy, *Hoplostethus atlanticus* Collett, Smith et al. (1995) found that sectioned-otolith ages exceeded whole-otolith ages after the age of reproductive maturity. Ferreira and Russ (1994) found in the Great Barrier reef coral trout, *Plectropomus leopardus* (Lacépède), that the mean difference between sectioned-otolith and whole-otolith readings remains within one year in fishes up to 12 years, but increases abruptly to almost four years for age groups 13 and 14. Pearson et al. (1991) found that whole-otolith ages tend to be as much as eight years less than broken-and-burnt otolith ages in the short-belly rockfish, *S. jordani* Gilbert. In *L. peru*, discrepancies between whole-otolith and sectioned-otolith ages were not extreme, but whole-otolith age determinations were not reliable beyond the 15th annulus. It would be useful to extend these observations to other populations of *L. peru* to assess the variability of this pattern.

The coefficient of determination of the multiple regression model is affected by the degree of colinearity of the independent variables. Although not all the assumptions required for the use of a multiple regression model are met by the data set, including homoscedasticity, this does not preclude its results to serve as a first-order age approximation. Otolith weight appears to be a very good predictor of age in this species, as it has been observed in *P. leopardus* (Ferreira and Russ, 1994). The model was used to estimate the age of those otoliths that had been discarded as unreadable and for which all variables were available, placing the predicted ages very close to the VBGF curve (Fig. 7B). The success of this method suggests that it could be implemented for routine age determination of this species.



**Figure 7**

(A) Scatter plot of all length-at-age data used for VBGF parameter estimation. Length-at-whole-otolith age (circles), length-at-sectioned-otolith age (triangles), and VBGF curve obtained from this study (solid line). (B) VBGF curve from this study (solid line) and lengths at age reported in other studies of age and growth of *Lutjanus peru*. Mean observed lengths at age (open circles) and mean back-calculated (dotted open circles) from Ruiz et al. (1985); mean observed length at age from Aguilar Salazar (1986) (squares), mean observed length at age from Castro (1981) (triangles). Diamonds joined by a dotted line indicate the von Bertalanffy growth curve reported by Gutierrez Vargas (1990). Filled circles represent age estimates obtained with the multiple regression model for "unreadable" otoliths.

## Growth

The growth of *L. peru* was satisfactorily described by the generalized VBGF. The absence of a significant difference in mean length-at-age between sexes and the significantly different growth parameters might seem contradictory. However, the graphic representation of the data revealed that both sexes have very similar growth schedules during

the first 10–12 years (Fig. 5). The very few males sampled beyond the ascending limb of the curve may have prevented a more constrained curve fit in this region.

The results of this and other studies made in Mexico and Costa Rica reveal the following patterns: 1) scale-based studies, using traditional methods for growth parameter estimation, yield higher growth rates resulting from age underestimation if large fishes are involved (Table 5, reference A) but not so if only small fishes are included (Table 5, reference B); 2) small asymptotic lengths may result from a restricted length range (Fig. 7B); 3) length-frequency

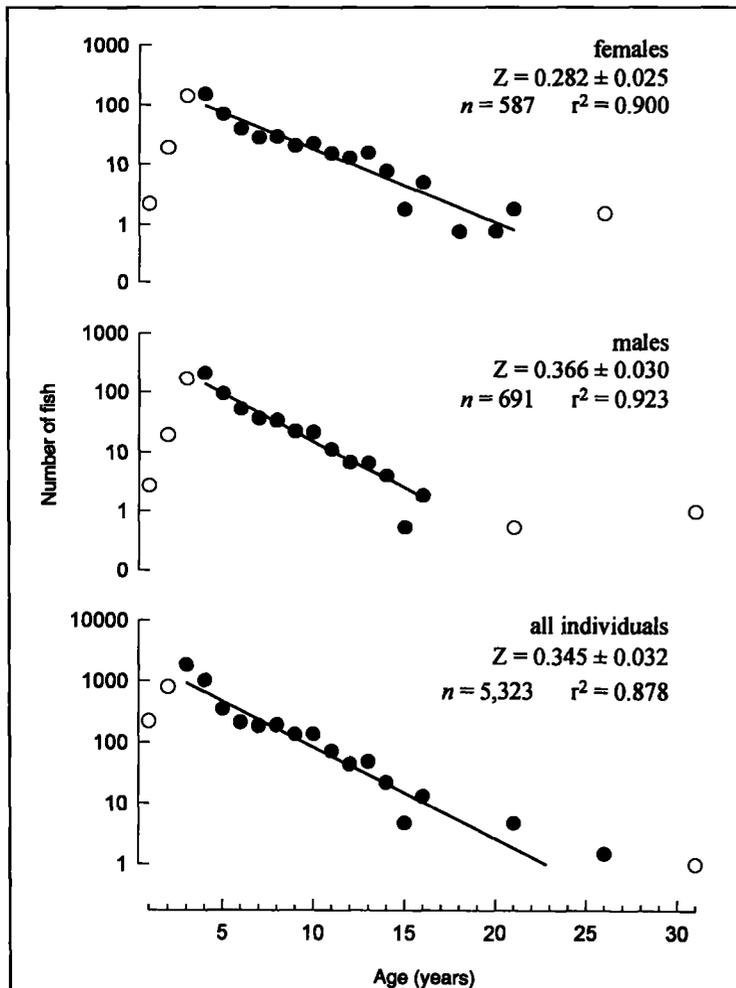
based methods for growth parameter estimation yield fewer age classes and unrealistic growth rates, which have been observed elsewhere (Grimes, 1987; see also Rocha Olivares, 1991, for examples of unpublished data). It is possible that part of the observed differences in the growth parameters of *L. peru* between peninsular and continental populations are “true”; however the diversity of fishing gears and selectivities used in different states (Aguilar Salazar, 1986) and the poor effort invested in systematic biological data collection make interpopulation comparisons difficult.

The presence of an individual of ca. 100-cm TL represents a length record for the species. The sectioned otolith age of this fish (31 years) also constitutes a record for the maximum age of an eastern Pacific lutjanid, and adds *L. peru* to the list of long-lived snappers (i.e. exceeding 30 years of age): *L. bohar* (38 years), *L. adetti* (37 years), *L. sebae* (35 years) (Loubens, 1980), *L. malabaricus* (46 years) (Mathews and Samuels, 1985), and *L. quinquelineatus* (32 years) (Newman et al., 1996). When compared with the growth trends observed in the family, growth performance of *L. peru* ( $\phi=1.74$ ) falls above the mean value for lutjanids (1.65) but within the expected range (1.08–2.15; SD=0.35) (Munro, 1983). Furthermore, the combination of  $L_{\infty} = 97.32$  cm and  $K = 0.1111/\text{yr}$  of the Baja California population of Pacific red snapper is very close to the functional relationship of  $\log_{10}(K)$  versus  $\log_{10}(L_{\infty})$  reported by Manooch (1987) for snappers (Lutjanidae) and groupers (Serranidae).

**Mortality**

In this study, estimates of *M* were restricted to the use of empirical relationships between *M* and *K* because no effort data were available and no unfished areas could be sampled. It has been repeatedly observed that these two parameters are inversely related across a large number of fish taxa (Pauly, 1980). Hoenig’s (1983) empirical formula yielded an unrealistically low estimate of mortality, as it probably would in other long-lived snappers. When compared to total mortality rates (*Z*), estimates of *M* are consistent and yield much lower exploitation rates and *F/M* ratios than those reported for other lutjanids (cf. Table 8.2 in Ralston, 1987), probably as the result of an overestimation of *M* by the empirical formulae.

Male predominance in population sex ratios is not uncommon among lutjanids (cf.



**Figure 8**

Catch curves and estimates of total mortality of *Lutjanus peru* females, males and sexes combined, caught by hook and line off the southeast coast of Baja California Sur. The age composition was computed with an age-length key and the length composition of the massive and biological samples. Total mortality rates *Z* (per year ± standard error) are presented for females, males, and the entire population. Black dots represent data points included in the calculation of the slope (solid line).

Table 5.1 in Grimes, 1987). Populations of *L. peru* studied in Baja California Sur and Michoacán off continental Mexico show this bias (1:0.82,  $n=785$ ; Ruiz Luna et al., 1985). In lutjanids, evidence suggests that skewed sex ratios probably reflect differ-

ential growth and mortality between sexes (Grimes, 1987). Other reproduction studies on lutjanids have also suggested a tendency for females to be more common at larger sizes. The population sampled in this study shows significant differences in mortality rates

**Table 4**

Age-length key used in the construction of the catch curves of Pacific red snapper, *L. peru*. Ages represent whole-otolith ages except for fish older than 15 years for which sectioned otoliths were used.

Length Group (cm)	Age group (year)																				Total			
	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+	16+	18+	20+	21+		26+	31+	
10.1-15.0	15	8																						23
15.1-20.0	1	107	2																					110
20.1-25.0		50	69	8																				127
25.1-30.0		1	58	62																				121
30.1-35.0			4	102	17																			123
35.1-40.0				40	70	7																		117
40.1-45.0				9	67	37	2																	115
45.1-50.0					17	53	26	2	1															99
50.1-55.0					1	9	47	26	6		1													90
55.1-60.0						6	8	24	23	10	3													74
60.1-65.0							3	11	20	9	11	3	1											58
65.1-70.0								1	6	17	20	7												51
70.1-75.0								2	5	6	4	10	8	7	1									43
75.1-80.0											1	2	3	6	1	1	2				1			17
80.1-85.0											1		1		4		1							7
85.1-90.0																		1	1			2		4
> 90																							1	1
Total	16	166	133	221	172	112	86	66	61	42	41	22	13	13	6	1	3	1	1	1	1	2	1	1180

**Table 5**

Comparison of growth parameters of *Lutjanus peru* obtained in studies from Mexico and Costa Rica (F-W=Ford-Walford plot, NL=nonlinear regression,  $n$ =sample size, LFA=length-frequency analysis, obs=observed lengths, back=back-calculated lengths, NA=not applicable).

	Reference						
	A		B		C	D	E
Study site	Michoacan		Michoacan Guerrero Oaxaca		Baja California Sur (Los Cabos region)	NW Costa Rica	Baja California Sur (Bahía de La Paz region)
Structure used	scales		scales		scales	NA	otoliths
Method	F-W		F-W		F-W	LFA	NL
Data	obs.	back	obs.	obs.	back	NA	obs
$L_{\infty}$ (cm)	81.5	79.5	82.64		66.71	83.34	92.85
$K$ (per yr)	0.196	0.191	0.11		0.23	1.46	0.12
$t_0$ (yr)	0.725	0.786	1.48		-0.54	0.04	0.14
$n$	1068	412	175		208	5902	1180
Age range (yr)	1-7	1-7	0-2		0-8	1-12	0-31
Size range (cm)	23-62	24-64	21-37		20-59	24-82	10-99

A = Ruiz et al. (1985); B = Aguilar Salazar (1986); C = Castro (1981); D = Gutierrez Vargas (1990); and E = this study.

between sexes. The higher mortality rate of males may account for the biased sex ratio. In no other lutjanid species has such a large difference in total mortality been observed between males and females. Whether this difference results from different availability to the fishing gear, spatial segregation, or foraging behaviors (*F*-associated difference), or from differences in predator vulnerability or natural longevity (*M*-associated difference) requires further research.

In this paper I have compared the merit of scales, whole otoliths, and sectioned otoliths to age the Pacific red snapper, *L. peru*. As is the case for other tropical and semitropical fishes, the usefulness of whole-otolith age determination is limited up to a certain age, after which, sectioned otoliths are the only reliable method for ageing and scales should be avoided. Age determinations from whole and sectioned otoliths of fishes covering most of the known size range of *L. peru* were used to determine the VBGF parameters. A 31-year-old fish measuring 99.2 cm is reported and constitutes a record size and age. Total mortality rates were higher for males resulting in a preponderance of females among the older fishes.

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