Age and Growth of the Leopard Grouper, Mycteroperca rosacea, in the Southern Gulf of California, México¹

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Abstract: Growth of the leopard grouper, Mycteroperca rosacea (Streets, 1877), was analyzed in its natural habitat. Age determination was based on the reading of otoliths, and the method was validated under three main criteria: (1) proportionality, (2) seasonality, and (3) concordance with another method. Otolith growth is proportional to organism growth, with a slight degree of allometry, and the otolith registers the growth of the individual, even at advanced ages. The opaque growth zone in the otolith is deposited once a year, between July and October. Thus, taken together, one opaque and one hyaline mark represent an annual cycle. Back-calculated lengths-at-age agreed reasonably well with observed lengths-at-age at the time of capture, considering that back-calculated lengths represent an exact age (birthday), and observed lengths are taken at an intermediate age between birthdays. Fish length and otolith age data were fitted to the von Bertalanffy growth function by two methods: (1) linear regression (Ford-Walford and Beverton), using transformed data, and (2) nonlinear regression, by iteration. Although the nonlinear regression gave a fit with unbiased error, parameters resulting from linear regressions had a better biological meaning for the species. The resulting parameters were compared with those reported for other species of the family Serranidae.

The Leopard Grouper, Mycteroperca rosacea (Streets, 1877), is found in subtropical shallow coastal waters, in a restricted geographical area from Magdalena Bay (Baja California

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Sur) to Banderas Bay (Jalisco), including the Gulf of California (Thomson et al. 1987, Heemstra 1995). The family Serranidae forms an important part of the catches from the artisanal fishery of Baja California Sur, and the leopard grouper surpasses other species both in volume and frequency of catches (Rodríguez-Medrano 1990). The biology of the leopard grouper is poorly known. There are works referring to its description and taxonomic status (Rosenblatt and Zahuranec 1987), distribution and abundance in La Paz Bay, B.C.S. (Villavicencio 1983), and feeding habits (Bermúdez-Almada and García-Laguna 1985), but previous studies on age and growth for this species are lacking.

Individual growth rate, age structure, and age of first maturity and recruitment are useful parameters for the evaluation of populations, and the confidence level at which they are estimated depends, in large part, on the method used for age determination (Ricker 1979, Sparre and Venema 1992). The reading of scales and otoliths has been the most frequently used method for age determination of fish. In slow-growing, long-lived

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species, the growth marks are unreadable near the edge of scales, causing an underestimation of age. Otoliths have proven more useful for age determination in this kind of organism (Boehlert 1985, Devries and Frie 1996). Considering the long life cycle and slow growth rate of species composing the family Serranidae (Manooch 1987), we considered that otoliths would be the most reliable structure for age and growth analysis of the leopard grouper. Even the reading of otoliths does not ensure a priori that this method of age determination is dependable. It must be demonstrated that the marks used to determine age are related to a specific time interval, and that they can be observed for most of the life cycle of the species (Beamish and McFarlane 1983, Casselman 1983). Only in this way can the bias in estimation of growth parameters be reduced, or at least known, and the consequences in resource appreciated (Beamish management McFarlane 1983).

The von Bertalanffy growth function has proven to be a good model in studies of growth because of the applicability of its parameters in more complex models describing population dynamics (Sparre and Venema 1992). Because of the commercial importance of the leopard grouper, the estimation of growth parameters is especially valuable because of its relevance to fishery management. In this study we analyze the validity of otolith reading for age determination of *Mycteroperca rosacea* caught in the Bay of La Paz, B.C.S., and vicinities, and the fitting of data to the Von Bertalanffy growth function is also presented.

MATERIALS AND METHODS

From January 1991 to June 1992 individuals of *M. rosacea* were selected monthly from both commercial and experimental catches made around Espíritu Santo and Cerralvo Islands, located off the western coast of the Gulf of California (Figure 1). A maximum of 15 fish per length interval (50 mm), per month, was randomly selected from the catches. Each fish was measured in total (TL) and standard (SL) lengths and gutted weight

(GW). Whenever possible, total weight (TW) and sex were also determined. After measuring, both *sagittae* otoliths were extracted by an oblique cut at the cranial basis. At the laboratory, otoliths were washed with soap and tap water and stored dry.

Before age determination, a small subsample of otoliths was subjected to different combinations of high temperatures (300–400 °C) and times (5–30 min) to improve the contrast between marks (Elorduy-Garay and Díaz-Uribe 1994). The temperature-time combination with best contrast was chosen and applied to all otoliths considered in the study.

Otolith readings and measurements were made using a dissecting microscope, an ocular micrometer, and reflected illumination, at 10× total magnification. Reading consisted of the counting of growth marks and the determination of edge type (i.e., opaque or hyaline). Each otolith was read twice independently. When both readings were identical the otolith was declared readable, and the number of marks (rings) and edge type were assigned to the corresponding fish. Whenever there were differences, otoliths were submitted to a third reading. If the third reading agreed with either of the previous two readings it was assigned as definitive; if not, the otolith was considered unreadable and discarded.

Three types of morphometric relationships were analyzed: TL versus SL, GW versus TW, and TL versus GW. The first two were evaluated using linear regression by least squares and Student's t-test under the null hypothesis $a=0,\ b=0,\$ and $R^2=0$ ($\alpha=0.05$). The third relationship was evaluated by the potential model $Y=ax^b$ using nonlinear regression by least squares, with the program FISHPARM 3.1 (Prager et al. 1989); in this case, Student's t-test was ran under the null hypothesis b=3 and $R^2=0$ ($\alpha=0.05$).

The use of otoliths for age determination of *M. rosacea* was validated with three basic criteria (Beamish and McFarlane 1983, Casselman 1983):

(1) Proportionality between otolith growth and fish growth was tested by selecting a stratified subsample, as a function of fish

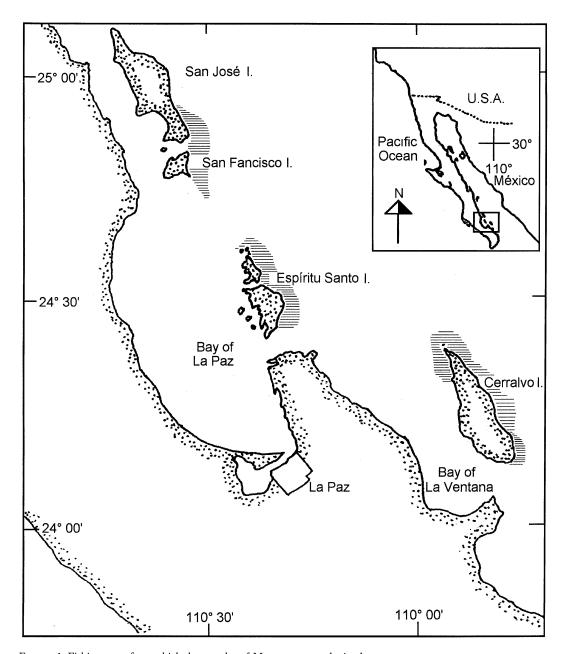


FIGURE 1. Fishing areas from which the samples of M. rosacea were obtained.

length and independent of the month of capture. A maximum of 20 pairs of otoliths per length interval was selected. The otoliths were measured in long diameter (OLD) and long radius (OLR). Data on otolith growth

and fish growth were adjusted to a potential model.

(2) Seasonality in the formation of growth marks was analyzed by the monthly frequency of otolith edge type, using the total sample. This information was compared with the sea surface temperature in southern La Paz Bay. The Secretaría de Desarrollo Social, Delegación B.C.S., kindly provided temperature data.

(3) Concordance with another method was analyzed by the back-calculation of lengths at past ages, as a reference method. The subsample used was the same as that used in the proportionality analysis. At this stage, the radii at each growth mark (annuli) were measured in each otolith. Average lengthat-age was estimated using the equation:

$$L_i = a^* R_i^b$$

where L_i is the length of the fish when the otolith radius was R_i ; a and b are the parameters of the regression of fish length on otolith radius from the proportionality analysis. Back-calculated lengths were compared with observed lengths at the time of capture.

Individual growth was calculated fitting the age-length data to the Von Bertalanffy growth function:

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

where L_t is the average length of the fish at age t; L_{∞} is the average maximum length of the analyzed stock; k is the growth coefficient; and t_0 is the parameter of origin of the growth curve.

Two separate methods were used to derive the growth function. In the first method (designated LRC) we followed the Ford-Walford procedure to calculate L_{∞} and the Beverton procedure to calculate k and t_0 (Ricker 1975, Sparre and Venema 1992). The second method utilized a nonlinear regression analysis (NLR) with the program FISHPARM 3.1 (Prager et al. 1989). Confidence intervals ($\alpha = 0.05$) were calculated for each parameter and compared with those calculated by the LRC method.

RESULTS

In total 769 fish were sampled during the study period, except for the months of June, November, and December 1991 when catches were low, and it was impossible for us to survey at sea. Individuals in the sample ranged from 283 to 975 mm TL, but 90% of the fish were between 350 and 700 mm TL (Figure 2). Sex was determined for 16% of the sample, comprising fish 286-808 mm in length (TL). None of the fish had virginal gonads.

Because of the small dispersion of data, the linear model fitted to the TL-SL relationship explains nearly 98% of the variability (P < 0.01) (Table 1). The GW-TW relationship presented the same behavior, with 99% ($\hat{P} < 0.01$) of explained variance (Table 1). Ordinates at the origin were not significantly different from zero (P > 0.05) in both regressions. Therefore, the standard length of the leopard grouper represents an average of 86-88% of the total length, and the gutted weight represents an average of 87–90% of the total weight.

The potential model fitted to the TL-GW relationship explains 97% of the observed variability (P < 0.01), so it has an important predictive value. The coefficient b = 2.97 is not significantly different from 3 (P > 0.05), so the leopard grouper exhibits isometric growth (Table 1).

Heating the otoliths at 325 °C for 25 min was the combination that rendered best results. Under these conditions, opaque rings turned yellow, and hyaline ones turned dark brown. The immersion of these otoliths in glycerin several minutes before the readings notably improved the contrast between rings. Nearly 95% of the otoliths were used in age determinations. The remaining were considered unreadable, because of lack of agreement in the number of rings (2%) or lack of agreement both in the number of rings and edge type (3%).

Otolith growth is strongly correlated to overall fish growth. All the correlation coefficients (r) were significant (P < 0.01), in spite of the fact that data present higher dispersion than the previous regressions (Table 2). In every correlation where TL is involved the exponent is significantly greater than 1 (P < 0.01), whereas in every correlation where GW is involved the exponent is significantly different from 3 (P < 0.01). This means that there is a certain degree of allom-

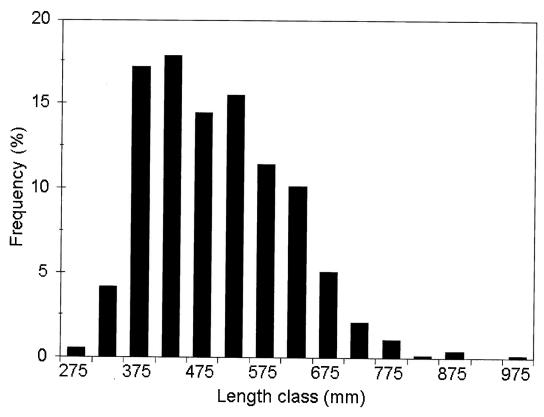


FIGURE 2. Frequency distribution of size classes (TL) for the whole sample of M. rosacea.

etry, in which the fish grows proportionally faster than the otolith.

In 1991 the frequency of individuals with opaque otolith edges was low in January and February and highest between July and October (Figure 3). Although there is no information for June, November, and December

in that year, the tendency in the other months indicates that individuals with opaque otolith edges predominated (>50%) from June to November. The frequency of individuals with opaque otolith edges was again low at the beginning of 1992. This pattern follows the temperatures registered in the Bay of La Paz.

 $\begin{tabular}{ll} TABLE\ 1 \\ Morphometric\ Relationships\ Involving\ Body\ Length\ and\ Weight\ in\ \emph{M. rosacea} \\ \end{tabular}$

Relationship						
	n	а	SE (a)	Ь	SE (b)	R^2
TL – SL GW – TW TL – GW	762 111 762	$ \begin{array}{c} -10.583 \\ 5.997 \\ 1.43 \times 10^{-5} \end{array} $	$12.998 120.312 1.58 \times 10^{-6}$	0.872 1.128 2.970	4.36×10^{-3} 8.51×10^{-3} 1.70×10^{-2}	0.981 0.994 0.973

Note: Total length (TL) – standard length (SL) (function, y = a + bx); gutted weight (GW) – total weight (TW) (function, y = a + bx); total length (TL) – gutted weight (GW) (function, $y = ax^b$). R^2 , coefficient of determination; n, sample size.

TABLE 2
Morphometric Relationships between Otolith Features and Body Length and Weight in M. rosacea

Relationship	Parameters						
	a	SE (a)	b	SE (b)	R^2		
OLD vs. TL	10.640	1.416	1.656	0.055	0.8360		
OLR vs. TL	34.640	3.276	1.639	0.055	0.8357		
OLD vs. GW	0.088	0.035	4.241	0.159	0.7928		
OLR vs. GW	1.538	0.452	4.288	0.161	0.7977		

Note: All relationships were fitted to the potential model $y = ax^b$. Linear dimensions are expressed in mm and weight in g. OLD, otolith long diameter; OLR, otolith long radius; TL, fish total length; GW, fish gutted weight, n = 187 for all cases.

In general, the temperature increase correlates well with the increase of opaque otolith edge development and vice versa. There is no evidence of another season with a high degree of opaque otolith edge development in the population. Thus, a set of one opaque and

one hyaline ring represents a year in the life of these fish.

The back-calculation of lengths at past ages showed that the readings on otoliths were consistent, except for the age groups of 12 or more years. In these, the back-

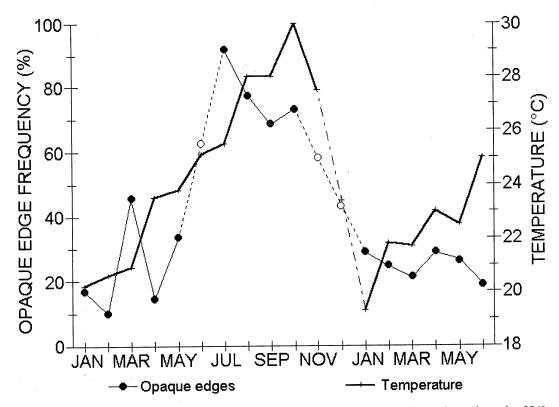


FIGURE 3. Monthly frequency of individuals of *M. rosacea* exhibiting opaque otolith edges in the total sample of 769 fish, plotted with mean monthly sea surface temperature in the Bay of La Paz.

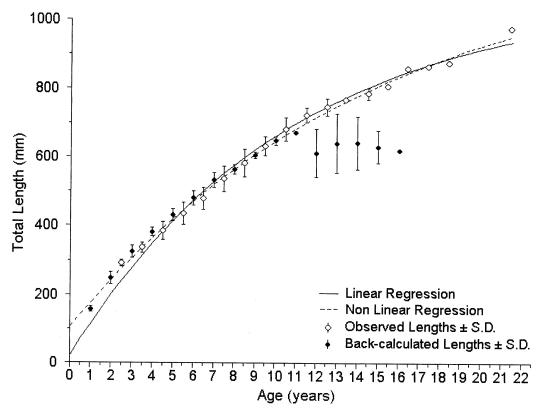


FIGURE 4. Growth curves (in total length, TL) of the leopard grouper fitted by two methods: NLR (nonlinear regression), using FISHPARM 3.1 (Prager et al. 1989) and LRC (linear regression). Back-calculated lengths-at-age (closed circles), and observed lengths-at-age (open circles) are shown.

calculated lengths were, on average, shorter than for the other age groups (Figure 4). Because of the small number of fish older than 11 yr, it is not possible to evaluate if the bias in the averages was due to a random factor or to an intrinsic factor of the otolith (Table 3).

The growth model was fitted to a set of data containing the back-calculated lengths-at-age, up to 11 yr, and the observed lengths-at-age (Table 4). Estimated parameters in the LRC method were different from those in the NLR method (Table 5). According to the standard error estimated by the NLR method, L_{∞} could vary from 1142 to 1310 mm (df = 28; P = 0.05); the $L_{\infty} = 1083$ estimated by the LRC method is outside that range. The growth coefficient k also showed differences between the two estimation

methods. The 95% confidence interval for k estimated by the NLR method is 0.0567 to 0.0750 yr⁻¹; the value of k (0.0925 yr⁻¹) estimated by the LRC method is outside this range. Although the nonlinear regression analysis (NLR) explains a larger amount of the variance in the data set, the goodness of fit should be evaluated in view of the biological information of the species (Figure 4).

DISCUSSION

Although sex could be determined only for a small number of fish, we can state that juveniles were not present in the sample. Even the smaller fish in our samples were adults, which agrees with the reports of Heemstra (1995), who referred to juveniles of *M. rosacea* as

 $\begin{tabular}{ll} TABLE 3 \\ Back-Calculated Lengths at Specified Ages for M. rosacea \\ \end{tabular}$

		Annuli															
n	Age Group	I	II	Ш	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI
2	2	172	270														
18	3	164	271	342													
32	4	162	265	342	392												
23	5	152	244	329	390	442											
18	6	158	251	325	380	427	483										
23	7	150	232	312	383	450	505	555									
15	8	150	227	304	366	418	470	530	579								
9	9	147	223	288	353	396	445	494	555	609							
10	10	164	234	306	362	416	465	526	552	609	656						
7	11	172	263	338	384	428	469	512	553	592	634	671					
2	12	155	191	229	270	309	354	403	442	484	527	572	623				
1	13	172	249	336	383	432	462	505	550	594	628	664	700	737			
1	14	172	249	291	336	383	423	462	505	550	594	628	664	700	737		
1	15	138	172	210	249	291	336	373	412	453	494	538	571	606	641	676	
1	16	138	172	210	240	274	309	336	364_	393	423	453	484	517	550	583	618
Wt	. Avg.	157	248	324	381	430	479	531	563	604	647	671	611	640	642	630	618
SD	3	6.82	16.41	16.52	12.16	16.01	19.01	20.77	12.59	7.74	10.88		69.07	85.84	76.61	46.59	477

Note: Weighted averages and standard deviations are shown. n is the number of fish in each age group. Underlined data were not used for averaging.

TABLE 4 Observed Mean Lengths of Individuals of M. rosacea at Various Ages as Determined by Otolith Annual Marks

Age (yr)	TL (mm)	SD	n
2+	291	7.616	4
3+	336	13.730	29
4+	385	25.232	142
5+	434	31.899	141
6+	477	30.924	98
7+	535	37.180	119
8+	582	39.179	84
9+	631	26.179	67
10+	681	32.472	24
11+	722	20.124	8
12+	747	23.629	3
13+	768	3.536	2
14+	786	15.556	2
15+	808	_	1
16+	860	_	1
17+	866	_	1
18+	875	_	1
21+	975		1

 $\it Note:$ TL, total length; SD, standard deviation of mean length; $\it n, sample$ size.

smaller than 300 mm TL. The same author reported a maximum length of 700 mm for the species, but Thomson et al. (1987) and Allen and Robertson (1994) mentioned that this species can reach up to 1000 mm and 12.2 kg of weight, although they did not specify the kind of length and weight. This

TABLE 5
Growth Parameters for *M. rosacea* Calculated by Two Regression Methods

	Nonl Regre		Linear Regression			
Parameter	Average	SE	Average	SE		
L_{∞}	1226	41.16	1083			
$\frac{-\infty}{k}$	0.06586	0.00447	0.09245	_		
	-1.393	0.1798	-0.2446	_		
r^2	0.99603	_	0.98034	_		

Note: L_{∞} in mm, k in year⁻¹, and t_0 in years.

divergence is shown in the length distribution found in our study sample. Although most individuals caught are less than 700 mm TL, larger fish are encountered; our study registered lengths to 915 mm TL, close to the maximum reported by Thomson et al. (1987) and Allen and Robertson (1994).

Heating otoliths is a useful technique to improve contrast and ease the reading of *M. rosacea* otoliths; each mark acquires a differential coloration.

The allometry phenomenon in the relationship of otolith size to fish size has been reported for several species, and discussed from the physiological point of view (Simkiss 1973). The extreme case in which otoliths grow to a maximum size and then grow only in thickness has been documented for several species of soles (Williams and Bedford 1973). In M. rosacea the evidence indicates that the fish grows at a higher rate than the otolith. The value of b = 1.656 indicates that when the fish increases its length 100%, the otolith grows approximately 53%. Other species, such as Ocyurus chrysurus (Manooch and Drennon 1987) and Lutjanus peru (Rocha-Olivares and Gómez-Muñoz 1993), have b values near 1.6. However, otolith growth does not completely stop in these cases. Although there are no precise criteria specifying the critical level at which allometry would adversely affect age determination by examination of otoliths, the values obtained for M. rosacea do not seem to cause problems, because even at the oldest ages, rings could be counted and measured.

Whenever growth marks are deposited periodically, it is possible to assess this process using the ratio of edge types (opaque or hyaline) in otoliths (Williams and Bedford 1973). The prevalence of opaque edges in summer–autumn and hyaline edges in winter–spring represents a defined pattern in *M. rosacea* otoliths.

We consider that reading of otoliths is a consistent method for determining age at the time of capture, because observed lengths were generally larger than back-calculated lengths at each age. Comparison was made taking into account that each method gives complementary information. That is, average

lengths by age at the time of capture represent the length at an intermediate age between two birthdays, because at the time of age assignment most otoliths show a fraction of edge, indicating that the birthday has already passed. However, back-calculated lengths at previous ages represent the exact birthday lengths. Therefore, the consistency of the two methods was analyzed by the following criteria: (1) each back-calculated length belongs to an exact age (1, 2, 3,..., etc.); (2) each length at the time of capture belongs to an intermediate age $(1.5, 2.5, \ldots,$ etc.). In this way, both data sets intercalate reasonably well between 3 and 11 yr of age, within what could be the individual growth curve. Because juveniles younger than 3 yr and adults older than 11 yr were scarcely represented in our sample, we consider only ages within this range to be accurately reflected by otolith characteristics.

Individual growth is a process that implies a change in body mass in a determined time period. To express this phenomenon in terms of length, von Bertalanffy developed his model under the hypothesis that organisms grow isometrically. That is, that the organism keeps the same body form during the growth period. Whenever this happens, the change in body mass or respiratory surface due to growth is proportional to the change in length cubed or squared, respectively. Pauly (1979) found that many fish species do not comply with this criterion, so the Von Bertalanffy growth model (VBGM) represents only a special case. The value of b = 2.97 in the leopard grouper is not significantly different from 3, therefore the use of the VBGM can be considered adequate in this case.

Fitting the growth curve by NLR is a statistically powerful method because no transformation of the data is required and the error of the parameters is estimated in an unbiased way (Prager et al. 1989). But this is a condition a priori, and the estimations must be evaluated as a function of the biological implications of the adjusted parameters. Several authors have discussed the close relationship of W_{∞} and k with the biological cycle of species (Pauly 1979, Manooch 1987, Sparre and Venema 1992). Munro and Pauly

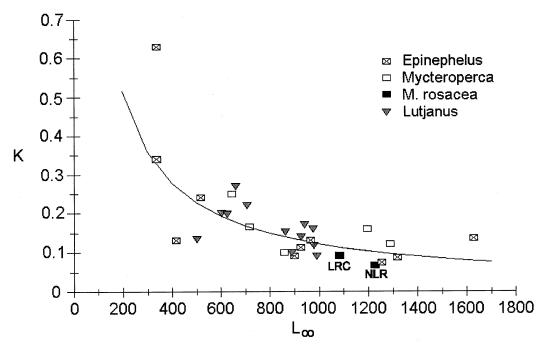


Figure 5. Growth performance (Φ) for several species of the families Serranidae and Lutjanidae (cited in Manooch 1987) and for *M. rosacea* by NLR (nonlinear regression) and LRC (linear regression).

(1983) developed the index $\Phi = \log k + 2/3 \log W_{\infty}$, called the "growth performance index" because it identifies specific kinds of growth in different taxonomic groups. An average value of $\Phi = 1.66$ has been estimated for the family Serranidae, varying from 1.35 to 2.26 (Manooch 1987). We estimated $\Phi = 1.735$ (using LRC) and $\Phi = 1.693$ (using NLR) (Figure 5). Both values are consistent with the "growth performance index" of the family Serranidae.

The asymptotic size of the model (expressed as L_{∞} or W_{∞}) has been generally defined as the average size a species would reach if growth were indefinite (Ricker 1975). Another interpretation was proposed by Pauly (1979), who argued that the asymptotic size should be equal to the average size of the oldest fish in a stock. The maximum length registered by us was 975 mm TL. It seems reasonable that the maximum length of 1000 mm reported by Thomson et al. (1987) is a good reference point of the asymptotic

length in the southern Gulf of California, following the concept of Pauly (1979). In this context, the value of $L_{\infty}=1083$ mm obtained by LRC seems more reasonable than the one estimated by the NLR method ($L_{\infty}=1226$ mm).

Manooch (1987) gave the values of k for the family Serranidae, which vary from 0.074 to 0.63 per year. The leopard grouper has k = 0.066 estimated by NLR, which is outside the range reported by Manooch, but the value estimated by LRC (0.092) is within the range.

It is important to stress that within the serranids the leopard grouper is one of the slowest growing species. This could be related to the feeding regime of the species. Buesa (1987) analyzed the growth rates of several species of demersal fish and found evidence that those with fish as a main item in their diet had slower growth rates than the ones with more diverse diets or the opportunistic ones. The leopard grouper has been

classified as fully piscivorous (Hobson 1965), but Bermúdez-Almada and García-Laguna (1985) found that, besides fish, *M. rosacea* also feeds on crustaceans in a 2:1 ratio (fish: crustaceans). In spite of utilizing foods with high energetic content, the low growth rates of fish with this feeding regime are due to the large energetic cost of searching and chasing prey (Buesa 1987).

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