

AGE AND GROWTH OF THE BLACKTAIL COMBER, *SERRANUS ATRICAUDA* (SERRANIDAE), OFF THE CANARY ISLANDS (CENTRAL-EASTERN ATLANTIC)

*Victor M. Tuset, José A. González, Ignacio J. Lozano
and M. Mercedes García-Díaz*

ABSTRACT

This study provides information about the age and growth of the blacktail comber *Serranus atricauda* Günther, 1874 from the Canary Islands, eastern-central Atlantic. The length-weight relationship was described by the following parameters: $a = 0.0056$ and $b = 3.25$, being positively allometric. Age was determined from annuli in whole otoliths (sagittae) stained with ninhydrin, which highlighted the alternating opaque and translucent zones of each annulus. The high percentage of otoliths with translucent zones during the annual cycle indicated that this species has continuous growth year-round. Age range was 2–16 yrs for fish measuring 16.2–43.2 cm TL, and weighing 55–1104 g TW. This species is slow-growing and long-lived. The growth parameters obtained were $L_{\infty} = 49.52$ cm TL, $K = 0.11 \text{ yrs}^{-1}$, and $t_0 = -0.76$ yrs. Otolith length was the best predictor of fish length, while the otolith weight was the best predictor of age.

The family Serranidae contains many bottom-dwelling predators of high commercial interest as fish food (Froese and Pauly, 2000). Genus *Serranus* is composed of 29 valid species (Froese and Pauly, 2000), which are usually synchronous hermaphrodites, a reproductive pattern considered to be the most primitive within the Serranidae (Smith, 1965). This special characteristic has been taken into consideration in detailed studies of the species: sexuality and reproduction (Reinboth, 1962, 1970; Atz, 1965; Fishelson, 1970; Febvre et al., 1975; Zanuy, 1977; Bruslé, 1983; Abd-el-Aziz and Ramadan, 1990; García-Díaz et al., 1997, 1999, 2001, 2002), feeding habits (Bell and Harmelin-Vivien, 1983; Benmouna et al., 1986; Arcuelo et al., 1993; Morato, 2000; Tuset et al., 1996, 1997; Moreno-López et al., in press), population differentiation (Dufossé, 1956; Oliver 1970, 1980; Tuset et al., 2002), and fisheries (Smith, 1981; Bauchot, 1987; Pérez-Barroso et al., 1993). However, studies on age and growth are scarce (Bouain, 1981; Abel-Aziz, 1991; Labropoulou et al., 1998; Tserpes and Tsimenides, 2001).

The blacktail comber *Serranus atricauda* Günther, 1874 is a littoral (3–150 m) benthic species, occurring from the eastern Atlantic (Bay of Biscay to Mauritania, the Azores, Madeira and the Canary Islands) and the western Mediterranean, with commercial interest in many regions (Smith, 1981, 1990; Bauchot, 1987). In the Canary Islands, it is an economically important species for small-scale inshore fisheries, although they are not reported in official fisheries statistics (Pérez-Barroso et al., 1993; Franquet and Brito, 1995). While details of its reproduction are known (García-Díaz et al., 1999, 2002), nothing is known about the age and growth of this serranid. The purpose of this study was to validate age estimates using the sagittal otolith, to derive fish growth rates, and to investigate the relationships among otolith, fish length, and age to assess the applicability of otolith dimensions in predicting the age of this species.

MATERIAL AND METHODS

Blacktail combers ($n = 510$) from the Canary Islands (central-eastern Atlantic) were sampled from October 1992 to April 1995. Samples were taken by a random stratified method from commercial catches of the local, artisanal, multispecific fisheries with fish traps, gillnets, longlines and handlines near the islands of Gran Canaria and Fuerteventura (Fig. 1).

Total length (TL, cm), total weight (TW, g), and gutted weight (GW, g) were measured for each fish. Relationships between total length-total weight and total length-gutted weight were calculated using a power function to fit the data (TW or $GW = aTL^b$). A t-test was used to determine if the slopes of both relationships were significantly different from three (Pauly, 1984).

Sagittal otoliths were used to obtain age and growth information. They were washed, dried, and stored in plastic vials. Otoliths were measured along two axes (length, OL, and width, OH, through the central nucleus) to the nearest 0.01 mm, with a digital counter and a data processor connected to a profile projector. To avoid mistakes in otolith weight (OW) due to water content, sagittae were oven dried, desiccated to a constant weight (Pawson, 1990), and weighed to 0.01 mg.

The methodology used for otolith reading is according to Tserpes and Tsimenides (2001), who used whole otoliths in *S. cabrilla*. Nevertheless, to find the best method for age determination, a random subsample of 20 individuals was studied, interpreting growth rings from whole otoliths and otolith sections. The results did not indicate differences between the reading methods, so age was estimated from whole otoliths. To increase contrast between bands, otoliths were stained with ninhydrin (Schneppenheim and Freytag, 1980). Otoliths were placed on a watch glass with a black-

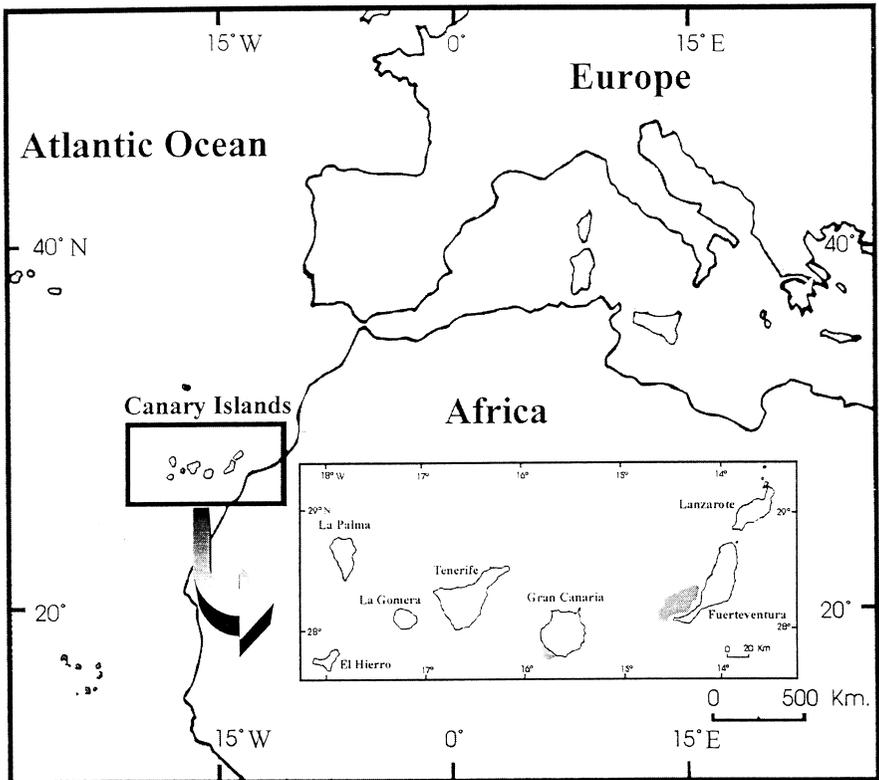


Figure 1. Location of sampling areas (□) in the Canary Islands.

ened bottom and examined under a compound microscope with reflected light. Two readers independently counted opaque zones in each otolith, and only coincidental readings were accepted. The symmetry test was applied to determine if there were systematic age-related differences among readers, or if differences were simple random error (Hoening et al., 1995). Ageing was validated indirectly by examining monthly changes in the appearance of the otolith margin (Morales-Nin, 1992). The first of June (peak spawning; García-Díaz, 2003) was considered the birth date. All fish were assigned an equal age or their annuli count, excluding fish collected prior to the first of June, which were assigned one year less than their number of annuli.

Because fish < 16 cm TL are usually not vulnerable to the fishing methods (see results), the mean length corresponding to earlier ages was determined by backcalculation (Francis, 1995). To carry out this technique, the relationship between otolith radius (OR) and total length (TL) was calculated using a power function, $TL = aOR^b$. Standardized residuals of the regression were analyzed to identify the type of estimate to use (biological or mathematical). Individuals were grouped in 4-cm TL classes and the homogeneity of residual variances was compared using the Levene's test (Zar, 1996); if residuals increased with fish length (heteroscedasticity), we could assume that the family of trajectories of individual growth was copunctual (Francis, 1995). In addition, to determine if otolith growth is proportional to somatic growth during the life cycle (Leeuwen and Rijnsdorp, 1986), the relationship between standardized residuals and age classes was also analyzed (Levene's test). According to these preliminary analyses, geometric mean regression was used to calculate total lengths at lower ages (Ricker, 1992). Mean sizes of each age class obtained by backcalculation and otolith readings were compared using the t-test (Francis, 1990; Zar, 1996).

Nonlinear regression among all available age-length data was used to estimate parameters of the von Bertalanffy growth equation,

$$L = L_{\infty} \left[1 - e^{-K(t-t_0)} \right]$$

where L is total length (cm), L_{∞} asymptotic length, K the growth coefficient, t the age (years) and t_0 the hypothetical age at which length is zero. To evaluate the effects of the age determination method used on growth parameter estimation, the von Bertalanffy growth equation was fitted to data collected by three methods: otolith readings, backcalculation, and a mixture of both. The last method is a combination of a representative sample of otolith reading (between three and 16 yrs) with data obtained by back-calculation (individuals aged 1–2 yrs). The Hotelling's T^2 test was used to compare the growth parameters obtained with each method (Cerrato, 1990; Gordo, 1996).

The relationships between otolith dimensions (length, width, and weight) and length or age of fish were determined by means of the lineal ($Y = a + bX$) or power function ($Y = aX^b$) depending on the best fitting; Y being the length or age and X as the otolith dimensions. No statistical differences (t-test, $P > 0.05$) were found between the dimensions (length, width, and weight) of right and left otoliths. Despite these similarities, right otoliths were used throughout to obtain these equations. However, when the right otolith was lost or broken during dissection, the left otolith was substituted. Each analysis was carried out for all individuals, since this species is a simultaneous hermaphrodite (García-Díaz et al., 2002).

RESULTS

LENGTH AND WEIGHT RELATIONSHIPS.—Individuals ranged between 16.2–43.2 cm TL, 55.3–1104.2 g TW, as well as 52.5–1043.6 g GW. The relationships between total and gutted weight and total length were (Fig. 2):

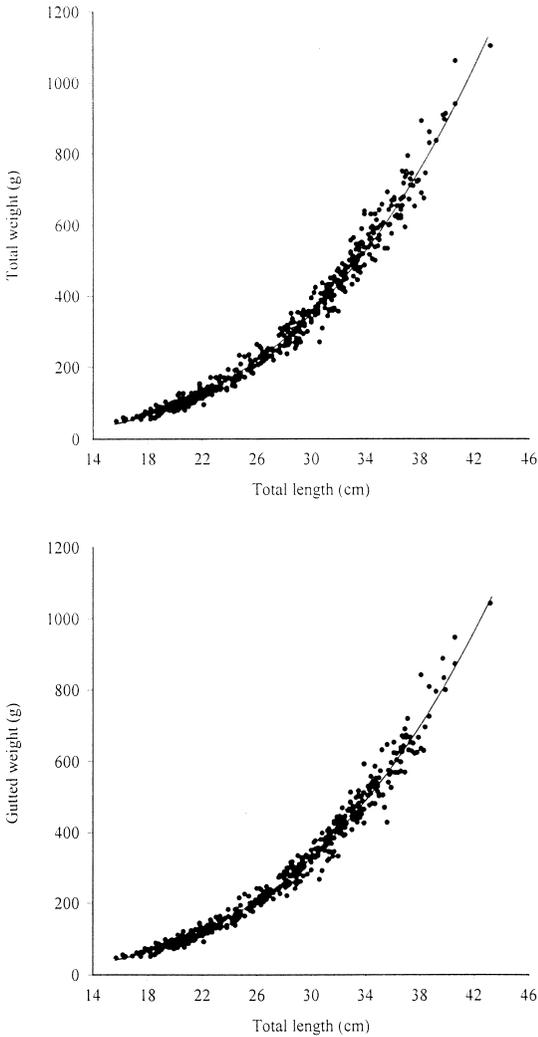


Figure 2. Somatic total weight-total length (upper) and gutted weight-total length (lower) relationships for *Serranus atricauda* from Canary Islands.

$$TW = 0.0056 * TL^{3.247}, r^2 = 0.986,$$

$$GW = 0.0062 * TL^{3.199}, r^2 = 0.988.$$

The slope ($b = 3.247$, $SE = 0.017$ for TW-TL regression; $b = 3.199$, $SE = 0.016$ for GW-TL regression) was significantly different from 3 (t-test, $t = 14.87$ and $t = 12.80$ respectively, $P < 0.05$) indicating positive allometric growth.

AGEING.—The annuli were clearly distinguishable and easy to count in whole otoliths, with the first annulus notably wider and more well-defined than subsequent annuli. Of the otoliths examined, 466 (91.4%) were readable with an 87.2% agreement between the

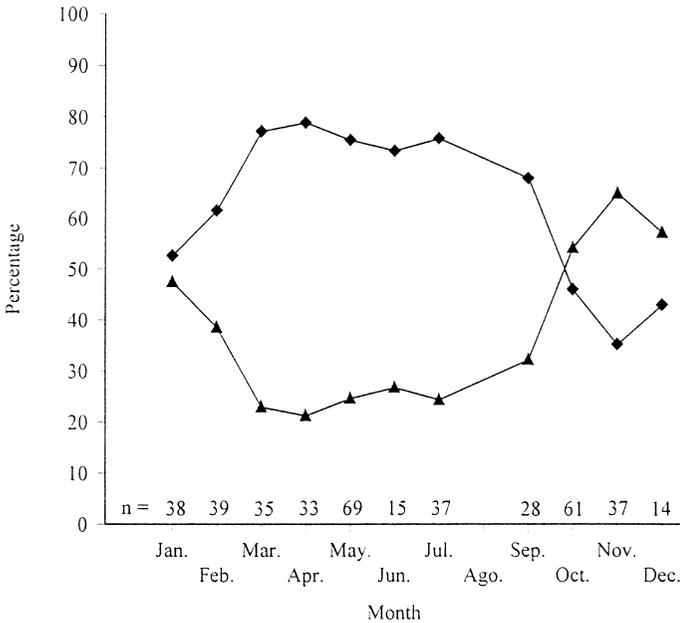


Figure 3. Mean monthly percentage of otoliths with opaque (i) and translucent (ó) edges for *Serranus atricauda* from Canary Islands.

two independent readers. The symmetry test did not indicate a systematic disagreement between readers ($X^2 = 7.01$, $P < 0.001$). Marginal zone analysis showed a pattern of alternating, narrow translucent zones, and wide opaque zones, forming one annulus per year (Fig. 3). Otoliths with an opaque edge (faster growth) were more abundant (54.1–64.9%) from October to December, while otoliths with a translucent edge (slower growth) were more common during the remaining months.

Fish ranged from 2–16 yrs (Table 1). Individuals < two yrs old were absent or poorly represented in the sample due to bias of the fishing method.

BACKCALCULATION.—The relationship between fish length (TL) and otolith radius (OR) was:

$$TL = 1.991 * OR^{1.243}, r^2 = 0.895 \text{ (Fig. 4).}$$

No significant differences were found in the standardized residual variance with fish size (Levene's test, $F = 1.54$, $P > 0.05$), but differences did occur with fish age ($F = 1.18$, $P < 0.05$). The homoscedasticity of data points around the regression line (Fig. 5) suggests that the regression equation is more appropriate than a proportional method, since there was no evidence for a common origin of individual growth trajectories. Otolith growth was allometric by the 10-yr age class (Fig. 5), so the backcalculation technique was only applied until the 9-yr age class.

The mean lengths by age class obtained by geometric mean regression are given in Table 2. Comparison between the mean lengths obtained by backcalculation and otolith

Table 1. Age-length key from the interpretation of growth rings on whole otoliths for *Serranus atricauda* from the Canary Islands. n - number of specimens; SD - standard deviation.

Length (cm)	Age (years)																
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
16			1	3													
17			1	2	5	3											
18				8	13	1											
19					20	4											
20					23	8											
21					8	17	3										
22					3	18											
23					3	6	4										
24						1	10										
25						1	8	2									
26						1	11	4									
27							5	4									
28							10	13	8								
29							6	10	6	1							
30							3	7	3	1	2						
31							2	11	8	4	5	1					
32								6	10	3	1	1					
33								5	7	4	4	4	3				
34									3	3	3		2				
35									1	2	4	2	2				
36									2	1	4	2	3				
37										1	1	3	1	1			
38												2	1				
39														1			
40													1				1
41																	
42																	
43																	1
Mean TL, cm	-	-	16.5	17.40	19.5	21.6	26.2	29.4	31.2	32.8	33.4	34.9	35.4	38.0	-	43.0	39.0
SD	-	-	0.7	0.9	1.4	1.9	2.4	2.1	2.2	2.0	2.1	2.3	2.1	1.4	-	-	-
n	-	-	2	13	75	68	62	62	48	20	24	15	13	2	-	1	1

reading in each age class revealed significant differences between both methods up to the 8-yr age class (Table 3).

FISH GROWTH MODEL.—To determine the best growth model, parameters obtained by otolith reading, backcalculation, and the mixture method were compared. In otolith reading, only fish aged > 2 yrs were considered. Backcalculation was carried out using the mean length until the 8-yr age class and the age-length key for the older ones. The mixture method included the reading data of age classes > 2 and data from backcalculation length for age classes < 3. The growth parameters of von Bertalanffy equation are presented in Table 4.

The comparison of the three methods pointed out significant differences in the growth parameters between otolith reading and the other methods (Hotelling's T^2 -test reading-mixture $T^2 = 17.93$, $P > 0.05$; reading-backcalculation $T^2 = 11.80$, $P > 0.05$), while

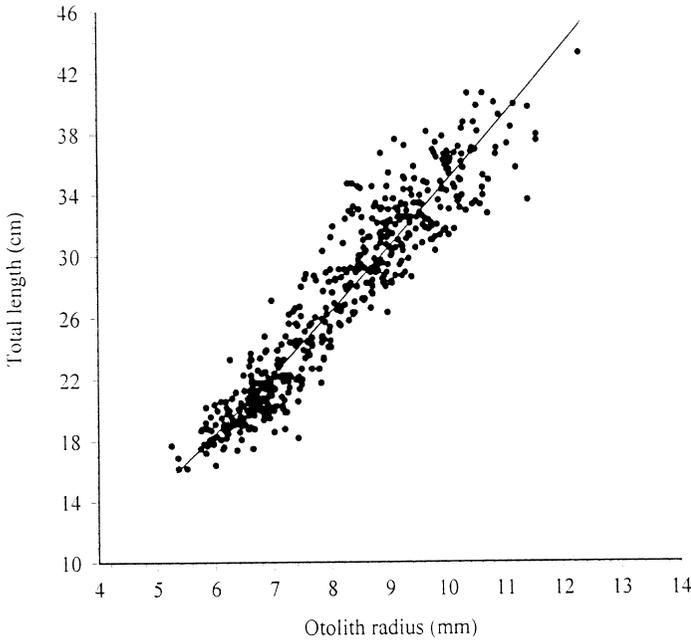


Figure 4. Relations between size fish (TL) and otolith radius (OR) for *Serranus atricauda* from Canary Islands.

backcalculation and mixture methods provided similar values (Hotelling's T^2 -test = 1.68, $P < 0.05$). Nevertheless, the mixture method produced the lowest standard error of the three. The resulting growth model was:

$$TL = 49.518 * \left[1 - e^{-0.111 * (t + 0.762)} \right], r^2 = 0.935 \text{ (Fig. 6).}$$

OTOLITH GROWTH.—In all cases the power function was the best mathematical model describing the relationships between length/age and otolith dimensions, with the exception of the relationship between age and otolith weight. Otolith length was the best predictor of fish length ($r^2 = 0.895$) and otolith weight was the best predictor of age, alone accounting for 88% of the variability. All variables were good predictors of length or age, each explaining over 80% of the variability. The slope of the relationship between fish size and otolith length and width was > 1 , while the slope of fish size and otolith weight was < 1 . Variability in the data increased significantly for all variables beyond 30 cm TL or eight yrs (Table 5, Fig. 7).

DISCUSSION

Biological studies and dynamic population models used in the management of fishery resources require age data to determine the composition by age for catch and growth rates (Ricker, 1973). Some authors have indicated that reading whole otoliths underestimates

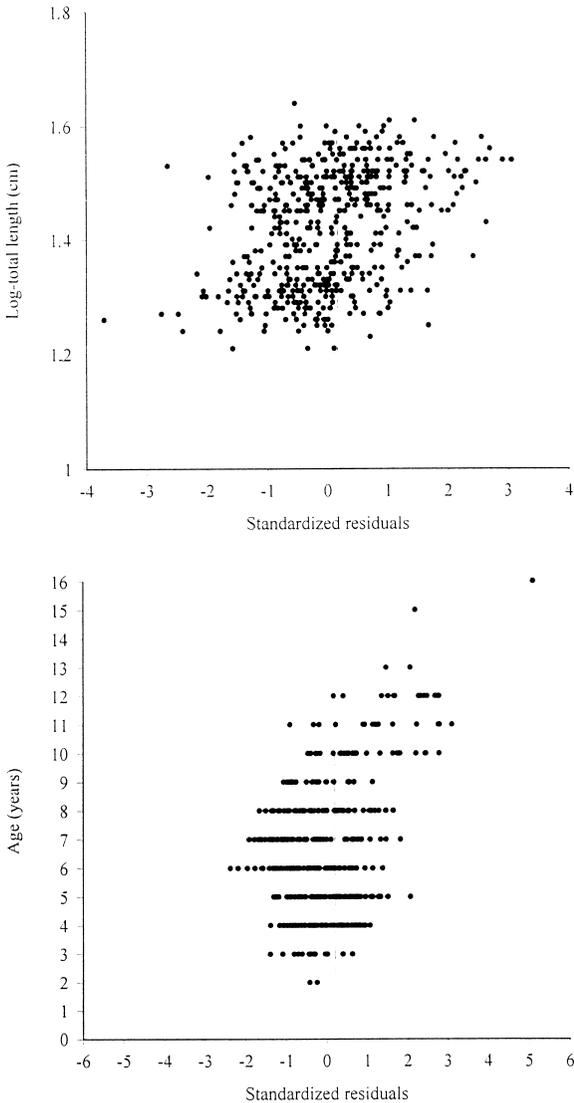


Figure 5. Residual plots of size fish (TL) versus otolith radius (OR) (upper) and age fish versus otolith radius (OR) (lower) relationships for *Serranus atricauda* from Canary Islands.

true age, as it is better to determine it in sectioned otoliths (Boehlert, 1985; Ferreira and Russ, 1994). However, there are alternative techniques such as staining (Albrechtsen, 1968; Liew, 1974; Bouain and Siau, 1988; Richter and McDermott, 1990) that enable the determination of age in some species using whole otoliths. The sagittal characteristics in *Serranus* spp. (Tuset et al., 2003) allows readings from whole otoliths as in *S. cabrilla* (Tserpes and Tsimenides, 2001). In our study, the symmetry test did not reveal differences among readers, suggesting both the ageing method and interpretation were correct and not age-dependent.

Table 2. Backcalculated length at age for *Serranus atricauda* from the Canary Islands. N - number of individuals; SD - standard deviation; Ri - mean length (TL, cm) for each age and annuli.

Age	Annulus									n
	R ₁	R ₂	R ₃	R ₄	R ₅	R ₆	R ₇	R ₈	R ₉	
2	9.85	13.50								2
3	9.92	13.55	16.49							13
4	9.48	13.16	16.27	19.15						75
5	9.40	12.99	16.31	19.22	21.89					68
6	9.71	13.00	16.27	19.56	22.22	23.56				62
7	8.63	12.27	15.66	18.67	21.69	24.46	27.05			62
8	8.85	12.70	16.74	19.38	22.29	24.94	27.13	29.65		48
9	8.06	11.52	14.77	17.71	21.07	24.58	26.70	29.49	32.15	20
10	9.52	12.99	16.09	18.94	22.37	25.04	27.48	30.28	33.36	24
11	9.51	12.37	15.56	18.12	21.20	23.39	25.94	28.61	31.08	15
12	9.63	13.62	16.09	19.37	22.37	24.43	26.86	29.34	31.88	13
13	8.05	10.79	14.51	18.53	22.80	25.48	28.24	31.07	33.99	2
14	-	-	-	-	-	-	-	-	-	-
15	8.71	12.99	16.89	17.70	21.93	24.58	27.31	31.08	33.01	1
16	8.82	12.78	16.42	17.25	21.15	23.45	26.52	29.47	32.52	1
Mean TL, cm	9.31	12.86	16.08	18.97	22.02	24.57	26.88	29.67	32.36	406
SD	9.4	10.3	1.10	1.23	1.17	1.26	1.31	1.38	1.72	

The blacktail comber is a relatively long-lived (maximum age 16 yrs) and slow-growing species. The high percentage of otoliths with translucent zones during the annual cycle indicates that this species exhibits continuous growth throughout the year. Environmental and biological variables such as temperature, photoperiod, feeding frequency and reproduction, as well as hydrological factors, may affect the annuli formation (Casselman, 1983; Campana and Neilson, 1985; Morales-Nin, 1992). This species does not exhibit variation in feeding over the year (Morato et al., 2000). Greater metabolic activity is observed when water temperatures are lower (fall–winter, Llinás et al., 1993), and the formation of the translucent zone coincides with the species' reported spawning period (January–September, García-Díaz, 2003). Nevertheless, the presence of annuli in immature individuals is empirically evident and suggests that the formation of annual rings is not dependent solely on the spawning season. Therefore, the stimulus for annuli forma-

Table 3. Comparison between mean sizes (TL, cm) obtained by otolith reading and backcalculation for *Serranus atricauda* from the Canary Islands. ($\alpha = 0.05$, * = $P < 0.05$).

Age	Mean TL (by otolith reading)	Mean TL (by backcalculation)	Difference	t-Student	Significance
2	16.5	12.9	3.6	7.32	*
3	17.4	16.1	1.3	5.17	*
4	19.5	19.0	0.5	3.23	*
5	21.5	22.0	-0.5	2.15	*
6	26.2	24.6	1.6	5.13	*
7	29.4	26.9	2.5	8.71	*
8	31.2	29.7	1.5	4.38	*
9	32.8	32.4	0.4	0.97	NS

Table 4. Von Bertalanffy growth parameters and respective standard errors (SE), and correlation coefficients (r^2) for the curve fitted to backcalculation, mixture and otolith reading method for *Serranus atricauda* from Canary Islands.

Method	L_{∞} (SE)	K (SE)	t_0 (SE)	r^2	n
Backcalculation	52.257 (4.038)	0.092 (0.016)	-1.053 (0.372)	0.989	15
Mixture	49.518 (1.650)	0.111 (0.007)	-0.762 (0.105)	0.935	490
Reading	43.875 (1.531)	0.160 (0.016)	0.158 (0.231)	0.871	406

tion may be correlated with those external factors, which also initiate spawning cycles in mature individuals.

It has been widely described that the morphology (especially weight) of the otolith, is related to changes in fish metabolism and is sensitive to variations in growth rates (Boehlert, 1985; Reznik et al., 1989; Secor and Dean, 1989; Pawson, 1990; Fletcher, 1991). In many fish species, otolith growth occurs primarily as increases in otolith thickness and weight, and to a lesser degree, in length and width (Blacker, 1974; Beamish, 1979; Janusz, 1990; Newman et al., 1996; present study). For example, in this study, otolith length and width were not as high as predicted for the largest fish (> 30 cm TL), while otolith weight was greater than predicted. The equation relating age to otolith weight and fish size revealed these differences in otolith length and width. Harkönen (1986) suggested that such a change might be due to a metabolic difference associated with sexual maturity. However, in this species the size of the metabolic change (30 cm TL) is higher than the maturity size (19 cm TL; García-Díaz, 2003). Ublein et al. (1998) concluded that these differences in size might be related to the fact that this species inhabits the shelf and uppermost parts

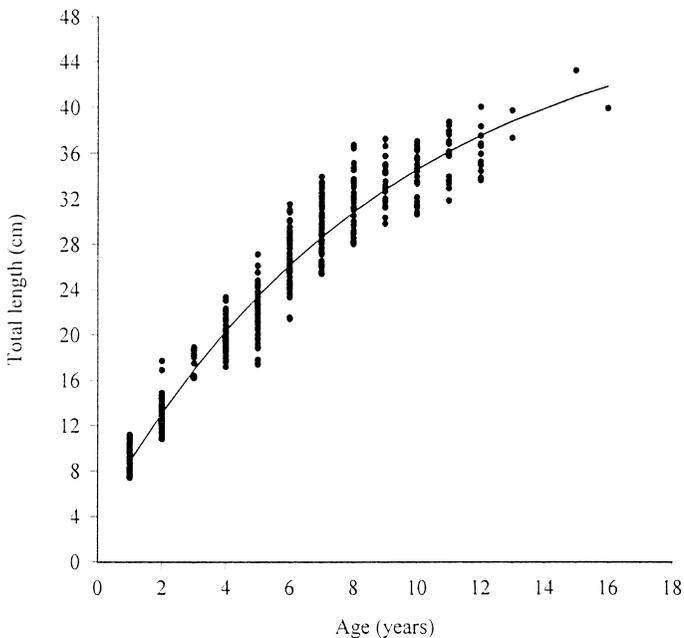


Figure 6. Von Bertalanffy growth curve fitted to length-at-age data of mixture method for *Serranus atricauda* from Canary Islands.

Table 5. Comparison between otolith dimensions and sizes and ages for *Serranus atricauda* from Canary Islands.

Equation	r ²	n
$TL = 1.991 * OL^{1.243}$	0.895	510
$TL = 5.802 * OH^{1.267}$	0.876	510
$TL = 18.583 * OW^{0.406}$	0.873	510
$Age = 0.127 * OL^{1.871}$	0.871	406
$Age = 0.640 * OH^{1.901}$	0.812	406
$Age = 2.362 + 1.552 * OW$	0.886	406

of the upper slope. Individuals > 30 cm TL moving to deeper waters may undergo an important metabolic change. In conclusion, the data suggest that sagittal otolith growth is asymmetric and somatic growth and otolith size are not coupled. Xiao (1996) considered it inappropriate to use terms as uncoupling, scaling, and time lag to describe the dependence of otolith size on somatic growth, and proposed the term relationship. Independently of the terminology applied, the strong correlation between otolith weight and age could indicate that this variable may provide a quick method for assessing age. The relationship between otolith weight and fish age has been verified for other fish species and appears to be a powerful, simple method to estimate the age of fish (Boehlert, 1985; Pawson, 1990; Cardinale et al., 2000; Labropoulou and Papaconstantinou, 2000). However, in some studies (including the present) both the increase of variability in otolith weight in older fish and frequent data points located off of the regression line from a determined age indicate that this variable may underestimate the age in older fish (Beckman et al., 1991; Wilson et al., 1991; Ferreira and Russ, 1994; Worthington et al., 1995; Newman et al., 1996).

A representative model of the growth of the average fish should be based on as wide a range possible of length-age values. The first years of life (juvenile phase) represent the period of fastest growth, after which the growth pattern changes considerably (Caddy, 1988; Morales-Nin, 1991; Labropoulou et al., 1998). However, in some studies, the growth curve represents only a portion of the population because sampling is truncated by fishing methods (e.g., Ferreira and Russ, 1994; Lorenzo and Pajuelo, 1999). It seems logical to apply all techniques available to complete the growth curve (Morales-Nin, 1984). The backcalculation technique is the usual method for increasing the number of length-at-age data used in fitting growth curves (Francis, 1990). To apply this technique, it is necessary to analyze the relationship between otolith length and fish size to identify the most applicable model (Esteves et al., 1997). Two factors have an influence in such a relationship: the allometric growth between both variables and the presence of slow-growing fish (with heavier otoliths) and fast-growing individuals (with lighter otoliths; Francis et al., 1993). The first factor reflects heteroscedasticity from a determined age while the second one leads to the assumption that individual growth trajectories are 'copunctual' (Eknath and Doyle, 1985; Heidinger and Clodfelter, 1987; Francis, 1995). When both factors are present, it is more appropriate to use a geometric mean regression than a proportional method (Ricker, 1992), as in this work. The results obtained in this study showed that the introduction of the backcalculation technique provided significant

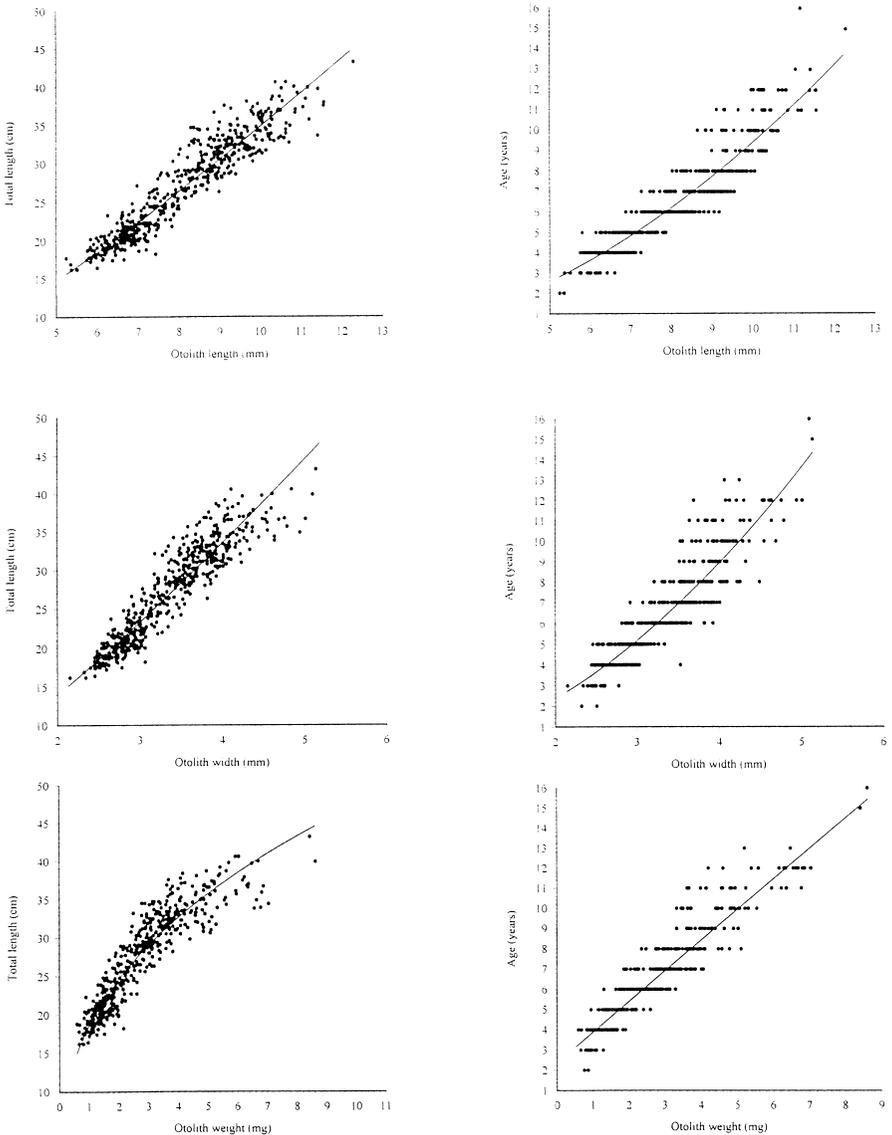


Figure 7. Relationship between total length/age and otolith dimensions (length, width and weight) for *Serranus atricauda* from Canary Islands.

variations in growth parameters. The growth parameters obtained by the mixture method were similar to those obtained by means of backcalculation; whereas, values from otolith reading were significantly different from the previous methods. Nevertheless, in the estimation of growth parameters, the mixture method provided values of standard error lower than those obtained by backcalculation. Consequently, the mixture model discussed here describes the fish growth better.

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LITERATURE CITED

- Abdel-Aziz, S. H. 1991. Sexual differences in growth of the painted comber, *Serranus scriba* (Linnaeus, 1758) (Teleostei, Serranidae) from southeastern Mediterranean. *Cybiurn* 15: 221–228.
- _____ and A. A. Ramadan. 1990. Sexuality and hermaphroditism in fishes. I. Synchronous functional hermaphroditism in the serranid fish *Serranus scriba* L. *Folia Morphol.* 38: 86–103.
- Abrechtsen, K. 1968. A dyeing technique for otolith age reading. *J. Cons. Perm. int. Explor. Mer* 32: 278–280.
- Arcuelo, M., C. Froglija and S. Riggio. 1993. Food partitioning between *Serranus scriba* and *Scorpaena porcus* (Perciformes) on the infralittoral ground of the south Tyrrhenian Sea. *Cybiurn* 17: 251–258.
- Atz, J. W. 1965. Hermaphroditic Fish. *Science* 150: 789–797.
- Bauchot, M. L. 1987. Serranidae. Pages 1301–1319 in W. Fischer, M. L. Bauchot and M. Schneider, eds. Fiches FAO d'identification des espèces pour les besoins de la pêche. (Révision 1). Vol II: Méditerranée et mer Noire; zones de pêche 37. FAO-CEE, Rome.
- Beamish, R. J. 1979. Differences in age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. *J. Fish. Res. Bd Can.* 36: 141–151.
- Beckman, D. W., A. L. Stanley, J. H. Render and C. A. Wilson. 1991. Age and growth-rate estimation of sheepshead *Archosargus probatocephalus* in Louisiana waters using otoliths. *Fish. Bull.* 89: 1–8.
- Bell, J. D. and M. Harmelin-Vivien. 1983. Fish fauna of French Mediterranean *Posidonia oceanica* seagrass meadows. 2. Feeding habits. *Tethys* 11: 1–14.
- Benmouna, H., M. F. Jaspas-Versali, C. Toussaint and C. Jeuniaux. 1986. A comparative study of chitinase activity in digestive tract of *Serranus cabrilla* and *Serranus scriba*. *Biochem. Syst. Ecol.* 14: 435–437.
- Blacker, R. W. 1974. Recent advances in otolith studies. Pages 67–90 in F. R. H. Jones, ed. Sea fisheries research. Elek Science, London.
- Boehlert, G. W. 1985. Using objective criteria and multiple regression models for age determination in fishes. *Fish. Bull.* 83: 103–117.
- Bouain, A. 1981. Les serrans (téléostéens, serranidés) des côtes sud de la Tunisie. Taille de première maturité, période de reproduction. *Cybiurn* 5: 65–75.
- _____ and Y. Siau. 1988. A new technique for staining fish otoliths for age determination. *J. Fish Biol.* 32: 997–978.
- Bruslé, S. 1983. Contribution to the sexuality of a hermaphroditic teleost, *Serranus hepatus* L. *J. Fish Biol.* 22: 283–292.
- Caddy, J. F. 1988. Comments of yield calculation presented at recent GFCM Technical Consultations on fish stock assessment. *FAO Fish. Rep.* 412: 201–206.
- Campana, S. E. and J. D. Neilson. 1985. Microstructure of fish otoliths. *Can. J. Fish. Aquat. Sci.* 42: 1014–1032.
- Cardinale, M., F. Arrhenius and B. Johnsson. 2000. Potential use of otolith weight for the determination of age-structure of Baltic Cod (*Gadus morhua*) and plaice (*Pleuronectes platessa*). *Fish Res.* 45: 239–252.
- Casselman, J. M. 1983. Age and growth assessment of fish from their calcified structures: techniques and tools. *NOAA Tech. Rep. NMFS* 8: 1–17.

- Cerrato, R. M. 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Can. J. Fish. Aquat. Sci.* 47: 1416–1426.
- Dufossé, A. 1956. De l'hermaphroditisme chez certains vertébrés. *Annls. Sci. Nat.* 5: 295–334.
- Eknath, A. E. and R. W. Doyle. 1985. Maximum likelihood estimation of “unobservable” growth and development rates using scale data: application to carp aquaculture in India. *Aquaculture* 49: 55–71.
- Esteves, E., J. Aníbal, H. Krug and H. Marques da Silva. 1997. Aspects of age and growth of bluemouth, *Helicolenus dactylopterus dactylopterus* (Delaroche, 1809) from the Azores. *Arquipélago* 15: 83–95.
- Febvre, M., M. Michele and M. Lafaurie. 1975. Comparaison de la séquence ovogénétique chez des Téléostéens ovipares gonochoriques et hermaphrodites (*Mullus*, *Serranus*, *Boops*). *Pubbl. Staz. Zool. Napoli* 39: 140–152.
- Ferreira, B. P. and G. R. Russ. 1994. Age validation and estimation of growth rate of the coral trout, *Plectropomus leopardus* (Lacepède, 1802), from Lizard Island, Northern Great Barrier Reef. *Fish. Bull.* 92: 46–57.
- Fishelson, L. 1970. Protogynous sex reversal in the fish *Anthias squamipinnis* regulated by the presence or absence of a male fish. *Nature* 227: 90–91.
- Flecher, W. J. 1991. A test of the relationship between otolith weight and age for the pilchard *Sardinops neopilchardus*. *Can. J. Fish. Aquat. Sci.* 48: 35–38.
- Francis, R. I. C. C. 1990. Back-calculation of fish length: a critical review. *J. Fish Biol.* 36: 883–902.
- _____. 1995. The analysis of otolith data — A mathematician’s perspective (What, precisely, is your model?). Pages 81–95 in D. H. Secor, J. M. Dean and S.E. Campana, eds. *Recent developments in fish otolith research*. University of South Carolina Press, Columbia.
- Francis, M. P., N. W. Williams, A. C. Price, S. Pollard and S. G. Scott. 1993. Uncoupling of otolith and somatic growth in *Pagrus auratus* (Sparidae). *Fish. Bull.* 91: 159–164.
- Franquet, F. and A. Brito. 1995. Especies de interés pesquero de Canarias. *Consejería de Pesca y Transporte del Gobierno de Canarias, Santa Cruz de Tenerife* 143 p.
- Froese, R. and D. Pauly. 2000. *FishBase 2000: concepts, design and data sources*. ICLARM, Los Baños, Laguna. 344 p.
- García-Díaz, M. M. 2003. Aplicación de técnicas histológicas para la determinación de aspectos reproductores en tres teleosteos marinos (Serranidae, *Serranus*). University of La Laguna Press, La Laguna. 228 p.
- _____, V. M. Tuset, J. A. González and J. Socorro. 1997. Sex and reproductive aspects in *Serranus cabrilla* (Osteichthyes: Serranidae): macroscopic and histological approaches. *Mar. Biol.* 127: 379–386.
- _____, M. J. Lorente, J. A. González and V. M. Tuset. 1999. Comparative ultrastructure of spermatozoa of three marine teleosts of the genus *Serranus*: *S. atricauda*, *S. cabrilla* and *S. scriba*. *J. Submicrosc. Cytol. Pathol.* 31: 503–508.
- _____, _____, _____ and _____. 2001. Application of histology in reproductive biology of fishery studies. Pages 1095–1100 in H.J.T.H. Goos, R.K. Rastogi, H. Vaudry and R. Pierantoni, eds. *Perspective in comparative endocrinology: Unity and diversity*. Monduzzi Editore, Bologna.
- _____, _____, _____ and _____. 2002. Morphology of the ovotestis of *Serranus atricauda* (Pisces, Serranidae), studied by light and electron microscopy. *Aquat. Sci.* 64: 87–96.
- Gordo, L. S. 1996. On the age and growth of bogue, *Boops boops* (L.) from the Portuguese coast. *Fish. Manage. Ecol.* 3: 157–164.
- Härkönen, T. 1986. Guide to the otoliths of the bony fishes of the northeast Atlantic. Edit. Danbiu. Hellerup. 256 p.
- Heidinger, R. C. and K. Clodfelter. 1987. Validity of the otolith for determining age and growth of walleye, striped bass, and smallmouth bass in power plant cooling ponds. Pages 241–251 in R. C. Summerfelt and G. E. Hall, eds. *Age and growth of fish*. Iowa State University Press, Ames.

- Hoening, J. M., M. J. Morgan and C. A. Brown. 1995. Analysing differences between two age determination methods by tests of symmetry. *Can. J. Fish. Aquat. Sci.* 52: 364–368.
- Janusz, J. 1990. Differences in the growth of otoliths of walleye pollock *Theragra chalcogramma* from the Bering Sea and the Gulf of Alaska. *Bull. Sea Fish. Inst.* 5–6: 13–18.
- Labropoulou, M., G. Tserpes and N. Tsimenides. 1998. Age, growth and feeding habits of the brown comber *Serranus hepatus* (Linnaeus, 1758) on the Cretan shelf. *Estuar. Coast. Shelf Sci.* 46: 723–732.
- _____ and C. Papaconstantinou. 2000. Comparison of otolith growth and somatic growth in two macrurid fishes. *Fish. Res.* 177–188.
- Leeuwen, P. I. and A. D. Rijnsdorp. 1986. The analysis of the growth of turbot by backcalculation of otoliths. *ICES* 35: 1–16.
- Liew, P. K. L. 1974. Age determination of american eels based on the structure of their otoliths. Pages 124–136 in T. B. Bagenal, ed. *The ageing of fish*. Old Working, Surrey: Unwin Brothers, London.
- Llinás, O., M. J. Rueda and E. Pérez-Martel. 1993. Variabilidad de parámetros oceanográficos en aguas de Canarias. *Bol. Inst. Esp. Oceanogr.* 9: 89–100.
- Lorenzo, J. M. and J. G. Pajuelo. 1999. Biology of a deep benthopelagic fish, roudi escolar *Promethichthys prometheus* (Gempylidae), off the Canary Islands. *Fish. Bull.* 97: 92–99.
- Morales-Nin, B. 1984. Aplicación del retrocálculo en la determinación del crecimiento de *Genypterus capensis* (Smith, 1847). *Colln. scient. Pap. int. Comm. SE. Atl. Fish.*, part. II: 7–12.
- _____. 1991. Parámetros biológicos del salmonete de roca *Mullus surmulletus* (L., 1758) en Mallorca. *Bol. Inst. Esp. Oceanogr.* 7: 139–147.
- _____. 1992. Determinación del crecimiento de peces óseos en base a la microestructura de los otolitos. *FAO Doc. Téc. Pesca.* 322: 1–58.
- Morato, T., R. S. Santos and J. P. Andrade. 2000. Feeding habits, seasonal and ontogenic diet shift of blacktail comber, *Serranus atricauda* (Pisces: Serranidae), from the Azores, north-eastern Atlantic. *Fish. Res.* 49: 51–59.
- Moreno-López, A., V. M. Tuset, J. A. González and M. M. García-Díaz. In press. Feeding ecology of *Serranus scriba* (Osteichthyes, Serranidae) in the marine reserve of Lanzarote (Canary Islands). *Bol do Mus Munic do Funchal*.
- Newman, S. J., D. M. B. Williams and G. R. Russ. 1996. Age validation, growth and mortality rates of the tropical snappers (Pisces: Lutjanidae) *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from the Central Great Barrier Reef, Australia. *Mar. Freshwater Res.* 47: 575–584.
- Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use programmable calculators. *ICLARM*: 1–325.
- Pawson, M. G. 1990. Using otolith weight to age fish. *J. Fish. Biol.* 36: 521–531.
- Pérez-Barroso, F. I., S. Jiménez, I. J. Lozano, J. A. González and J. I. Santana. 1993. Estudio preliminar de la pesquería artesanal de *Serranus atricauda* Günther, 1974 y de *Serranus cabrilla* (Linnaeus, 1758) (Osteichthyes, Serranidae) en el archipiélago canario. *Publ. Espec. Inst. Esp. Oceanogr.* 11: 365–373.
- Oliver, G. 1970. Recherches sur les Diplectanidae (Monogenea) parasites de Téléostéens du Golfe du Lion. III. Biologie. *Vie Milieu* 20: 397–420.
- _____, Y. Pichot and P. Pichot. 1980. Contribution à l'étude des serrans, *Serranus* Cuvier, 1817 (Pisces, Serranidae) de la réserve naturelle marine de Cerbère-Banyuls (Pyrénées-Orientales, France). *Rev. Trav. Inst. Pêches marit.* 44: 213–219.
- Reinboth, R. 1962. Morphologische und funktionelle Zweigeschlechtlichkeit bei marinen Teleostiern (Serranidae, Sparidae, Centranchidae, Labridae). *Zool. Jahrb. Art. Allg. Zool. Physiol. Tiere* 69: 409–480.
- Reinboth, R. 1970. Intersexuality in fishes. *Mem. Soc. Endocrinol.* 18: 515–543.
- Reznick, D., E. Linbeck and H. Bryga. 1989. Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). *Can. J. Fish. Aquat. Sci.* 46: 108–112.
- Richter, H. and J. G. McDermott. 1990. The staining of fish otoliths for age determination. *J. Fish. Biol.* 36: 773–779.

- Ricker, W. E. 1973. Linear regressions in fishery research. *J. Fish. Res. Bd Can.* 30: 409–434.
- _____. 1992. Back-calculation of fish lengths based on proportionally between scale and length increments. *Can. J. Fish. Aquat. Sci.* 49: 1018–1026.
- Schneppenheim, R. and G. Freytag. 1980. Age determination by staining otoliths of *Notothenia rosii marmorata* with ninhydrin. *Cybiurn* 8: 13–15.
- Secor, D. H. and J. M. Dean. 1989. Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatilis*. *Can. J. Fish. Aquat. Sci.* 46: 113–121.
- Smith, C. L. 1965. The patterns of sexuality and classification of Serranid fishes. *Am. Mus. Novit.* 22071: 1–20.
- _____. 1981. Serranidae. Pages 34, 47 in W. Fischer, G. Bianchi and W. B. Scott, eds. *Fiches FAO d'identification des espèces pour les besoins de la pêche. Vol I: Atlantique centre-est; zones de pêche.* FAO, Ottawa.
- _____. 1990. Serranidae. Pages 695–706 in J. C. Quéro, J. C. Hureau, C. Karrer, A. Post and L. Saldanha, eds. *Checklist of the fishes of the eastern tropical Atlantic. Vol II.* Unesco/ SEI/ JNICT, Portugal.
- Tserpes, G. and N. Tsimenides. 2001. Age, growth and mortality of *Serranus cabrilla* (Linnaeus, 1758) on the Cretan Shelf. *Fish. Res.* 51: 27–34.
- Tuset, V. M., A. Lombarte, J. A. González, J. F. Pertusa and M. J. Lorente. 2003. Comparative morphology of the sagittal otolith in *Serranus* spp. *J. Fish Biol.* 63: 1491–1504.
- _____, I. J. Lozano, J. A. González, J. Pertusa and M. M. Gracia-Díaz. 2002. Shape indices to identify regional differences in otolith morphology of comber *Serranus cabrilla* (L., 1758). *J. Appl. Ichthyol.* 19: 88–93.
- _____, J. A. González, M. M. García-Díaz and J. I. Santana. 1996. Feeding habits of *Serranus cabrilla* (Serranidae) in the Canary Islands. *Cybiurn* 20: 161–167.
- _____, _____, _____ and _____. 1997. Régimen alimentario de *Serranus cabrilla* (Linnaeus, 1758) (Osteichthyes, Serranidae) en el Atlántico oriental y Mediterráneo occidental. *Publ. Espec. Inst. Esp. Oceanogr.* 23: 181–185.
- Uiblein, F., F. Bordes, R. Castillo and A. G. Ramos. 1998. Spatial distribution of shelf- and slope-dwelling fishes collected by bottom longline off Lanzarote and Fuerteventura, Canary Islands. *Mar. Ecol.* 19: 53–66.
- Wilson, C. A., J. M. Dean, E. D. Prince and D. W. Lee. 1991. An examination of sexual dimorphism in Atlantic and Pacific blue marlin using body weight, sagittae weight, and age estimates. *J. Exp. Mar. Biol. Ecol.* 151: 209–225.
- Worthington, D. G., P. J. Doherty and A. J. Fowler. 1995. Variation in the relationship between otolith weight and age: implications for the estimation of age of two tropical damselfish (*Pomacentrus moluccensis* and *P. wardi*). *Can. J. Fish. Aquat. Sci.* 52: 233–242.
- Xiao, Y. 1996. How does somatic growth rate affect otolith size in fishes? *Can. J. Fish. Aquat. Sci.* 53: 1675–1682.
- Zanuy, S. 1977. Inducción a la puesta y estudio de la ovogénesis en un teleósteo marino: *Paracentropristis cabrilla* L. *Inv. Pesq.* 41: 337–384.
- Zar, J. H. 1996. *Biostatistical analysis*, 3rd ed. Prentice-Hall International, New Jersey 662 p.

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ADDRESSES: (J.A.G., M.M.G.-D.), *Instituto Canario de Ciencias Marinas, Departamento de Biología Pesquera, P.O. Box 56, E-35200 Tlede (Las Palmas) Canary Islands, Spain.* (I.J.L.) *Departamento de Biología Animal (U. Ciencias Marinas), Astrofísico F. Sánchez s/n. Universidad de La Laguna, Spain.*
 CORRESPONDING AUTHOR: (V.M.T.) *Instituto Canario de Ciencias Marinas, P.O. Box 56, E-35200 Tlede (Las Palmas), Spain. Telephone: +34-928 132 900, Fax: +34-928 132 908, E-mail: <Lepidopus@hotmail.com>.*