9165

Estimates of Age and Growth of Ehu *Etelis carbunculus* in Four Regions of the Pacific from Density of Daily Increments in Otoliths

M. Kimberly Smith
Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu, Hawaii 96822-2396
Present address: State of Hawaii, Department of Land & Natural Resources
Division of Aquatic Resources, 1151 Punchbowl St., Rm. 330, Honolulu, Hawaii 96813

Eric Kostlan
Department of Mathematics, University of Hawaii
Manoa Campus, Honolulu, Hawaii 96822

Abstract.– Growth of the deep slope snapper *Etelis carbunculus* was evaluated from the density of daily increments in sagittal otoliths collected from Hawaii, the Commonwealth of the Northern Marianas Islands (NMI), French Polynesia, and Vanuatu. The rate of otolith growth (μm/day) as a function of otolith radius was fit by regression to a modified Gompertz rate curve and the age of fish estimated by integrating the equation. There were slight regional differences between the estimated values of each of the three otolith growth rate parameters, which may be attributable in part to random sampling differences. However, integrated estimates of fish age versus otolith radius varied little between sites because of the compensatory relationship between two of the three estimated parameters which together determine the rate of dampening of the otolith growth function. There were significant regional differences in average otolith radius, and thus in estimated age, as a function of fish length. Fish from Vanuatu and NMI were younger at a given length than those from the other two regions. However, fish as large as those at Vanuatu are not found at NMI, suggesting there may be regional differences in mortality. Regional age-at-length data were fit to a von Bertalanffy growth curve, both unconstrained and held to a value of asymptotic length (L_∞) obtained from the literature. Estimates of natural mortality for each region are discussed, based on the regional values obtained for the von Bertalanffy growth constant (K). These results should be confirmed using data obtained from a wider range of fish sizes.

Manuscript accepted 11 February 1991.
Fishery Bulletin, U.S. 89:461–472 (1991).

The observation of microscopic markings in thin sections of the otoliths of fishes, with evidence that these marks present a record of daily growth (Panella 1971, 1974), provided an alternative means of ageing tropical species for which seasonal and annual growth rings are often hard to interpret. These marks are produced in many fishes (Brothers et al. 1976, Struhsaker and Uchiyama 1976, Wild and Foreman 1980, Neilson et al. 1985, Jones and Brothers 1987, and others). Counting otolith microincrements has proved useful in estimating the growth of juvenile and larval fishes (Barkman 1978, Methot 1981, McGurk 1984, Jones 1986, Geffen 1986), because they have small and transparent otoliths with readily interpretable microincrements. While offering the opportunity to detect growth on a more sensitive scale, the laborious process of enumerating all the daily increments in the otoliths of older organisms has limited the widespread use of this technique (Ralston and Williams 1988a).

From the late 1970s through the mid- and late 1980s, Ralston and colleagues (Ralston 1976, 1981, 1985; Ralston and Miyamoto 1981, 1983; Ralston and Williams 1988a) developed a labor-efficient method of estimating the age and growth rate of fishes using microincrement data from otoliths. This method, based on numerical integration of otolith growth rates from the density of presumptive daily increments, was applied by S. Ralston and H.A. Williams (Honolulu Lab., NMFS Southwest Fish. Sci. Cent., Honolulu, HI, unpubl. data) to a number of Pacific Ocean commercial species. It provided an estimate of the von Bertalanffy (1957) growth curve for which the asymptotic length (L_∞), growth constant (K), and age at zero length (t_0) were within the range of previous regional estimates for many of the 24 species for which the method was tested.

However, three out of four growth curves estimated by this method for the deep slope "red" snapper *Etelis carbunculus* (known as ehu in Hawaii), did not reach an asymptotic length, instead having the form of a straight line with positive slope. These results were considered to be anomalous, since collections included fish at or near the regionally estimated values of asymptotic length (although the sample size for some regions was very small). Otolith collections for this species came from Hawaii, Vanuatu, French Polynesia, and the

Commonwealth of the Northern Marianas Islands (NMI). In the single case where the estimated von Bertalanffy growth curve did reach an asymptote (379mm for NMI), it did so considerably below the maximum length commonly found in that region (580mm) and well below the maximum length included in the data.

The present study reevaluated the method of age and growth estimation using the same data, in an attempt to see if growth estimates could be improved. In response to some of the problems encountered in reprocessing the data, the methodology of integrating and fitting was modified in a manner that may prove useful to other researchers. In addition, some important guidelines for collecting data for growth estimation from integrated microincrement densities were developed.

Methods

Ralston and Williams' otolith growth data (unpubl.) from Hawaii, Vanuatu, French Polynesia, and NMI were reevaluated, using a new method that employs both analytical and numerical integration of the rate curve. Fork lengths were recorded and sagittal otoliths removed from fish caught with bottom handlines at depths of 80–200m in the four regions. The data were collected and compiled by Ralston and Williams from 1982 to 1988. They collected a wide size range of fish, but made no systematic sample of a representative number of organisms of each size. Small fish, not ordinarily captured with the large hooks used by commercial fishers, were underrepresented in all regional samples. Collections were essentially random, within the size range selected by this fishing gear. Since the principal objective was to find an appropriate method of fitting and integration, this limitation was acceptable.

Otoliths were prepared and microincrement densities on the postrostral axis recorded from video-relayed images using techniques described by Ralston and Williams (1988a). The data available for each fish included fork length, total otolith postrostral radius, and a series of estimates of microincrement density at various points along the otolith radius. Microincrement densities were registered in microns per increment, calculated by dividing the length of the radial segment by the number of increments counted within it. Following the assumption of Ralston and Williams (1988a) and Brouard et al. (1983) that microincrements are deposited on a daily basis for *Etelis carbunculus*, increment densities represent otolith growth rate (microns/day) as a function of distance from the origin of growth, or focus. Validation of daily increment deposition for most deep slope snappers has not been obtained because of low survival when fish are brought to the surface. However, validation was obtained for *Pristipomoides filamentosus* (Ralston 1981), another eteline snapper found in similar habitat and locations.

Ralston's method of age integration consists of estimating the time transpired within consecutive 500-μm intervals of otolith radius, by multiplying the length of each interval by its mean growth rate (microns/day). The estimated number of days required to grow through each 500-μm radial interval are then summed numerically, producing a series of estimated ages for fish with otoliths measuring 500, 1000, 1500μm, etc. The relationship between the natural logarithms of fork length and otolith radius, determined by regression from each regional sample, is then used to estimate fish length at the midpoint of each 500-μm interval of otolith radius. The resultant age-at-length data are fit to a von Bertalanffy growth curve by nonlinear regression. In this way, estimated fork lengths for a hypothetical group of fish with otoliths measuring 250–9250μm (by intervals of 500) are fit to age estimates for otoliths at 500–9500μm (by 500-μm intervals). Actual fork lengths and otolith measurements are used only to estimate the relationship between fork length and otolith radius. In addition to the slight difference in otolith radius (250μm) between age and length estimates, the validity of the assumption that the length of fish as a function of otolith radius can be accurately predicted from a regression curve obtained from the original sample depends on having had a representative size range and number of individuals from each population. Rather than incorporate this sampling error, it was decided to concentrate on using the otolith growth-rate data to obtain integrated age estimates for the fish and otoliths sampled.

Early attempts at integrating the otolith growth function were aimed at reducing the size of the radial interval used to approximate the growth rate. This was found to be impractical for various reasons. The average number of microincrement density estimates ("readings") per fish ranged from 4.1 to 61.5 regionally. Otoliths from Hawaii and French Polynesia were measured more extensively; 1681 and 3877 readings were made from 37 and 63 otoliths, respectively. For NMI and Vanuatu, fewer measurements were made (252 and 141 from 62 and 13 otoliths, respectively). Because of these differences in the number and distribution of microincrement density readings along the otolith radius, the reliability of mean otolith growth rates and resultant age estimates varied widely as a function of the length of the radial interval chosen. The asymmetry of the otolith growth-rate function compounded this problem. Therefore, an alternative method of integration that did not rely on mean microincrement densities as a function of radial intervals was chosen.

Estimates of otolith growth rate as a function of radius were fit by SAS (1985) nonlinear regression to a modified Gompertz rate curve (Gompertz 1825, Winsor 1932) of the form

$$y = axe^{-bx} + c \tag{1}$$

where y = estimated density of daily increments or otolith growth rate (μm/day),
x = radial distance (μm) at which each density was recorded,
a and b = shape parameters,
c = a constant representing the asymptotic otolith growth rate.

The Gompertz rate curve was chosen for its general shape and was then modified in form to provide a better fit to observed data. The constant was added because recorded microincrement densities did not subside to zero, instead reaching a low positive value.

Substituting dx/dt for y in equation (1) gives a clear picture of the otolith growth-rate function. Since the growth rate was estimated in days, the integral of the reciprocal of the righthand side of this function provides an estimate of the fish age in days as a function of otolith radius in microns, as follows:

Since $$dx/dt = axe^{-bx} + c$$

then $$t_x = \int_m^n \frac{dx}{axe^{-bx} + c} \tag{2}$$

where m and n are any two distances along the otolith radius. Substituting u = bx and du = bdx gives

$$t_x = \int_{mb}^{nb} \frac{du/b}{(au/b)e^{-u} + c} \tag{3}$$

$$= \frac{1}{cb} \int_{mb}^{nb} \frac{du}{(a/bc)ue^{-u} + 1}$$

$$= \frac{1}{cb} \int_{mb}^{nb} \{\sum_{k=0}^{\infty} ((a/bc)ue^{-u})^k (-1)^k\} \, du$$

$$= \frac{1}{cb} \sum_{k=0}^{\infty} (-1)^k \int_{mb}^{nb} [(a^k/b^k c^k) u^k e^{-ku}] \, du$$

$$= \frac{n-m}{c} + \sum_{k=1}^{\infty} \frac{(-1)^k a^k}{b^k c^k k^{k+1}} \Gamma(k+1, kmb)$$

$$- \sum_{k=1}^{\infty} \frac{(-1)^k a^k}{b^k c^k k^{k+1}} \Gamma(k+1, knb) \tag{4}$$

where Γ is the incomplete gamma function and k is a dummy variable. The first term, representing the asymptotic growth rate, is solved separately. Using the ratio test for convergence and an estimate based on the Gaussian continued fraction

$$V^k e^{-V} < \Gamma\,(k+1,\, V) < \frac{(V^{k+1} e^{-V})}{V-k} \tag{5}$$

(in Wall 1948), the first series converges for mb>M and the second for nb>M, where M is a solution of

$$\frac{M^2 e^{-M}}{M-1} = bc/va \quad \text{and } v \text{ is any number} > 1. \tag{6}$$

Thus, for each set of values of a, b, and c, a distinct point can be identified at which the expanded series converges quickly. For speed of computation, we chose v = 2, to ensure that the ratio of consecutive integrals would be less than 1/2. Age in days was estimated for each otolith radius by a Fortran program, adapted from Davis and Rabinowitz's (1984) routine for Romberg integration. Given values of x (otolith radius in microns), a, b, and c, the program first solves equation (6) by Newton's method (in Atkinson 1989) and then either uses the expanded series from equation (4), if it converges quickly, or evaluates the integral given in equation (3) by Romberg integration. Both estimates were made with a tolerance of 10^{-15}.

Fork lengths and estimated ages of the fish sampled were fit to the von Bertalanffy (1957) growth curve

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

where L_∞ and t_0 represent theoretical values of asymptotic length at infinite age and age at zero length, respectively; K is a growth constant; and t is fish age in years. The Marquardt method of iterative least-squares fitting was used, under SAS (1985) nonlinear fitting procedure. For comparison, the data were also fit by von Bertalanffy's method of log-linear regression, using a BASIC program by Gaschütz et al. (1988).

Table 1

Summary of otolith collections and maximum size of red snapper *Etelis carbunculus* by region.

		Fork lengths (mm)					
		Sampled				Recorded or estimated	
Collection site	No. of otolith	Min.	Max.	Avg.	SD	MLR*	ML_∞**
Hawaii	37	226	641	428.2	101.6	700 (1)	718 (5)
Fr. Polynesia	63	160	510	351.5	82.0	680 (2)	—
No. Marianas	62	29	527	337.5	66.3	540 (3)	537 (6)
Vanuatu	13	270	920	520.8	194.4	1270 (4)	993 (7)

---

*MLR = Maximum length recorded (from regional fishery statistics).

**ML_∞ = Average of three estimates of asymptotic length (L_∞) for the von Bertalanffy growth curve (from the literature).

Sources of MLR estimates

(1) United Fishing Agency, Ltd. (UFA), Honolulu, pers. commun., July 1988.
(2) Wrobel 1985
(3) National Marine Fisheries Service (NMFS), 1982-84. RAIOMMA Cruise data, unpubl. logs, NMFS Honolulu Lab.
(4) R. Grandperrin, ORSTOM fisheries biologist, Mission ORSTOM, New Caledonia, pers. commun., Feb. 1989.

Sources of ML_∞ estimates

(5) Ralston and Kawamoto 1987, Uchida et al. 1982
(6) Ralston and Williams 1988b, NMFS RAIOMMA data 1982-84
(7) Brouard et al. 1983, Brouard and Grandperrin 1985, Carlot and Nguyen 1989

Table 2

Estimated otolith growth-rate parameters and summary statistics for the modified Gompertz rate curve by region for red snapper *Etelis carbunculus*.

				Asymptotic correlation matrix		
Location		Parameter estimate	±95% CI	a	b	c
Hawaii	a	0.0688	±0.00311	1	0.741	−0.038
	b	0.0018	0.00005	0.741	1	0.499
	c	2.4242	0.22536	−0.038	0.499	1
			*R^2 0.713, n 1680,	**RSS 14211		
French Polynesia	a	0.0991	0.00357	1	0.764	0.006
	b	0.0021	0.00004	0.764	1	0.474
	c	2.4086	0.17919	0.006	0.474	1
			R^2 0.647, n 3877,	RSS 58776		
Commonwealth Northern Marianas	a	0.1111	0.01365	1	0.881	0.335
	b	0.0021	0.00014	0.881	1	0.624
	c	2.2672	0.43602	0.335	0.624	1
			R^2 0.824, n 252,	RSS 1251		
Vanuatu	a	0.0702	0.01180	1	0.866	0.204
	b	0.0019	0.00017	0.866	1	0.502
	c	2.1076	0.41886	0.204	0.502	1
			R^2 0.801, n 141,	RSS 467		
Overall (all locations combined)	a	0.0884	0.00250	1	0.765	0.012
	b	0.0020	0.00003	0.765	1	0.489
	c	2.3961	±0.13758	0.012	0.489	1
			R^2 0.661, n 5941,	RSS 76799		

---

*Multiple correlation coefficient $R^2 = [\Sigma(\hat{Y}_i - \bar{Y})^2/\Sigma(Y_i - \bar{Y})^2]$

**RSS = Residual sum of squares

Results

Number of otoliths, fish size range, and locations of collections are summarized in Table 1. For comparison, the maximum length registered in fisheries landings (MLR) and mean of available estimates of asymptotic length (ML_∞) for each region and their sources are also included. Intermediate sizes were represented in the data from most regions, but extremely large or small fish were underrepresented or lacking. The sample from Vanuatu was very small, but encompassed a wider range of fish lengths than was sampled from any other location. The limitations of the data must be kept in mind in interpreting and comparing results.

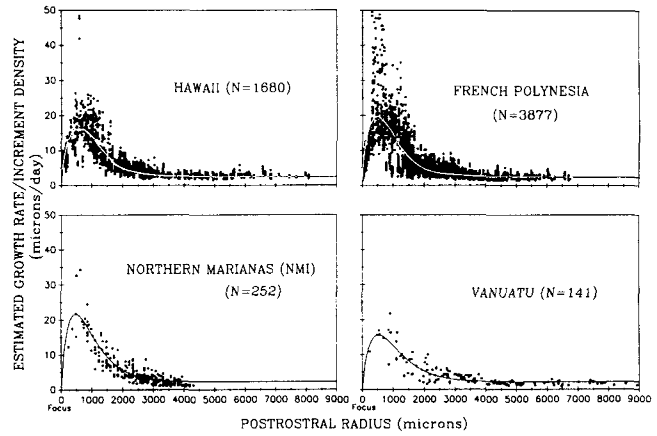

Figure 1
Estimated otolith growth rate and recorded microincrement densities for red snapper *Etelis carbunculus*.

Nonlinear regressions of otolith growth rate versus otolith radius in microns (Table 2) produced estimates of the parameters a, b, and c of the rate equation, with asymptotic 95% confidence intervals. Multiple correlation coefficients were calculated for each regression as an additional index of fit. Data were pooled for all locations to estimate a global rate for otolith growth. The multiple correlation coefficients are low for these curves, due to the wide range of variation in recorded increment density near the focus (high residual variance). Predicted curves and recorded microincrement densities for each region were compared (Fig. 1). The function chosen mimics the behavior of the rate curve fairly well; however, the fit could be improved in the descending portion of the curve between 500 and 1500μm of otolith radius. Few readings were made close to the otolith focus ($<246\mu$m) for NMI and Vanuatu samples (Fig. 1). Fitting the data to the rate curve assumes that these otoliths grew similarly to those for which the ascending portion of the curve was sampled. The fit for the descending portion of the curve is supportive of this assumption. However, since the widest range of variation in recorded microincrement densities was always found close to the focus, these results should be interpreted cautiously.

Predicted ages at equal otolith radius, using the parameters in Table 2, were calculated for each region (Table 3a). Although there were differences between the estimated regional otolith growth parameters, predicted ages as a function of otolith radius were generally similar. The relationship between the shape parameters a and b is such that differences between them can be compensatory, one (a) controlling the amplitude of the rate curve and the other (b) the rate of dampening. The radius at which peak otolith growth rate is estimated (the maximum of the otolith growth-rate function) was similar regardless of region or weighting. Peak growth rate occurs where the derivative of $axe^{-bx} + c$ is equal to zero, or at $x = 1/b$. Estimated ages for this radial distance are included in Table 3a, where it can be seen that the otoliths of ehu from all regions reach their maximal growth rate between 1 and 2 months of age. Otoliths reach a constant growth rate before fish are 1.5 years old, or between 3000 and 3500μm of otolith radius.

For comparison, the age estimates made by Ralston and Williams for comparable 500-μm intervals of otolith radius are given in Table 3b. The values are similar in many respects for Hawaii and French Polynesia (where more microincrement density estimates were made), but there are observable differences for all regions. Ralston and Williams' age estimates were lower close to the otolith focus, the two estimates were equivalent at intermediate radius, and their estimates were again lower at greater otolith radius. The exception to this pattern was seen for Vanuatu, for which our estimates were substantially lower at maximum radius. The radius at which the two estimates were equivalent and the magnitude of the difference between them varies from one region to another and is a function of the amount and variability of microincrement density readings and their effects on both estimates. The best check of which method gave more accurate results would be

Table 3A

Predicted ages at equal radial distances from estimated otolith growth rates for the red snapper *Etelis carbunculus*. NMI = Northern Marianas.

Otolith radius (μm)	Estimated age (days)				
	Hawaii	F. Poly.	NMI	Vanuatu	Overall
10	3.2	3.1	3.2	3.5	3.1
100	20.0	16.9	16.4	21.0	17.9
500	50.2	40.7	38.5	51.8	43.6
1000	82.4	68.6	65.3	85.7	72.8
1200	98	83	80	102	88
1400	116	101	98	122	106
1600	137	123	120	146	128
1800	163	150	147	174	154
2000	193	182	181	208	186
2500	290	292	298	319	292
3000	423	441	457	472	437
3500	586	619	648	657	611
4000	769	813	855	865	804
4500	964	1015	1071	1084	1005
5000	1164	1220	1289	1309	1211
6000	1573	1634	1729	1766	1627
7000	1985	2049	2170	2225	2044
8000	2398	2464	2611	2684	2461
9000	2810	2879	3052	3144	2878
10000	3223	3294	3493	3603	3296
11000	3635	3710	3934	4063	3713
12000	4048	4125	4375	4523	4130
13000	4460	4540	4816	4982	4548
14000	4873	4955	5257	5442	4965
	Age at 1/b μm of otolith radius				
Age (days)	555.5	484.8	467.7	532.5	504.8
1/b	53.5	39.9	37.0	53.9	43.8

Table 3B

Ralston and Williams' age estimates at equal otolith radius for the red snapper *Etelis carbunculus*.

Otolith radius (μm)	Estimated age (days)			
	Hawaii	F. Poly.	NMI	Vanuatu
500	46.7	40.7	25.1	37.5
1000	76.7	68.2	51.6	69.3
2000	193	191	172	211
2500	289	295	272	311
3000	422	416	418	433
3500	570	568	622	580
4000	758	764	866	759
4500	937	960	1250	1006
5000	1119	1157		1276
6000	1479	1571		1937
7000	1795	1955		2663
8000	2158			3181
9000				3997

to count all microincrements to a specific radius for the same otoliths. This was beyond the scope of the present study.

Fork lengths and age estimates, obtained by integrating the rate curve over the corresponding otolith radius (Appendix 1), were fit to a von Bertalanffy growth curve (Table 4). Both unconstrained regression and regressions with constraints on asymptotic length (L_∞) or age at zero length ($t_0 = 0$) were tested. Regressions with the highest indices of correlation were generally obtained by forcing the curve through an estimate of asymptotic length obtained from the literature or from regional fisheries statistics. The greatest value of MLR or ML_∞ from Table 1 for each region was used as an approximation of an appropriate forcing value. The criterion for convergence was based on a minimum level of improvement in the ratio of subsequent sum of squares errors (SSE):

$$(SSE_i - SSE_{i-1})/(SSE_i + 10^{-6}) < 10^{-8}.$$

Regressions which didn't converge after 200 iterations were eliminated. NMI was the only region for which the regression was able to converge with the constraint that $t_0 = 0$. Two fish from French Polynesia were omitted from the data, because their otolith radial lengths were not recorded.

Log-linear regressions using the Gaschütz et al. (1988) BASIC program were also done for comparison. These are weighted regressions of average age-at-length for NMI and French Polynesia, which had more than 50 observations. Figure 2 shows the best four growth curves (from Table 4). For all regions except NMI, these were the nonlinear regressions constrained in L_∞. The nonlinear method of fitting was preferred because it involved no artificial reduction of the variance observed in the data. For NMI the nonlinear regression constrained only to $t_0 = 0$ was used, because it had a higher r^2 value and lower residual variance. None of the curves for NMI showed a good fit; these results are included for comparison.

The scatterplot of age-at-length data (Fig. 2) illustrates the limitation on regression estimates imposed by the size range and number of fish sampled for each region. The most significant constraints on fitting a growth curve to the data were the high variance of estimated age (otolith radius) as a function of fork length, particularly for NMI and French Polynesia, and the limited range of fish sizes sampled. It was necessary to constrain most of the growth curves to an independently estimated value of L_∞, since there were few data points to represent extremely large or small fish. Although unconstrained curves could be fit to the data for Hawaii and French Polynesia, these reached values of L_∞ far above lengths of fish captured in these regions throughout the history of their fisheries. For NMI and Vanuatu, nonlinear regressions tended towards unlimited L_∞. These results were similar to those of Ralston and Williams, indicating that the primary limitation on accurate growth estimation was probably the range of fish lengths sampled.

Table 4

Summary of estimated growth by region for the red snapper *Etelis carbunculus*.

Region/Fitting assumptions	L_∞ (mm)	t_0 (yr)	K	R^2	RSS*
Hawaii (*N* 37)					
von Bertalanffy (unconstrained)	1182.8	2.06	0.064	0.920	30507
von Bertalanffy fix L_∞ = 718 mm	718.0	3.32	0.163	0.874	35005
von Bertalanffy fix L_∞ = 718 (linear**)	718.0	4.03	0.190	0.884	44250
Vanuatu (*N* 13)					
von Bertalanffy (unconstrained)	(no convergence)				
von Bertalanffy fix L_∞ = 1270 mm	1270.0	1.41	0.129	0.911	37503
von Bertalanffy fix L_∞ = 1270 (linear)	1270.0	1.62	0.137	0.920	39095
French Polynesia (*N* 60)					
von Bertalanffy (unconstrained)	1458.6	1.13	0.039	0.784	86365
von Bertalanffy fix L_∞ = 680 mm	680.0	2.35	0.126	0.756	89370
von Bertalanffy fix L_∞ = 680 (linear)	680.0	3.05	0.145	0.837	65115
Northern Marianas (*N* 62)					
von Bertalanffy (unconstrained)	(no convergence)				
von Bertalanffy (linear/unconstrained)	750.0	−0.18	0.179	0.576	115656
von Bertalanffy fix L_∞ = 540 mm	540.0	−0.23	0.289	0.435	142350
von Bertalanffy fix L_∞ = 540 (linear)	540.0	0.94	0.464	0.519	130986
von Bertalanffy fix L_∞ = 540, t_0 = 0	540.0	0.00	0.310	0.504	143137
von Bertalanffy fix t_0 = 0 (only)	583.2	0.00	0.273	0.572	142493

---

* RSS = Residual sum of squares.

** Linear = Log-linear regression and linear correlation coefficients from Gaschütz et al. (1988) BASIC program.

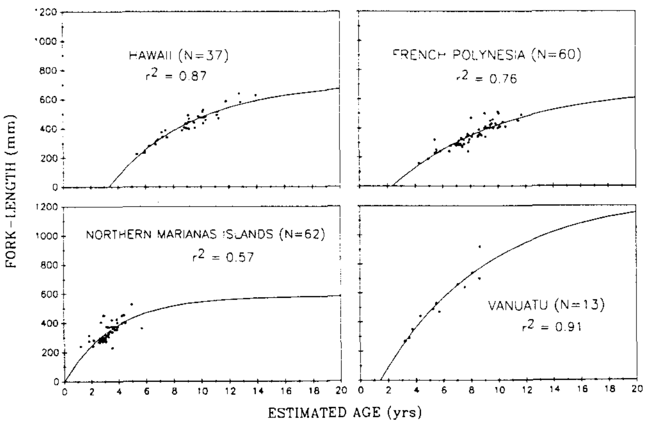

Figure 2

Estimated regional von Bertalanffy growth curves for red snapper *Etelis carbunculus*.

However, the present regressions differ from those of Ralston and Williams' in that they are derived from age estimates for measured otoliths and fork lengths, rather than from estimated lengths at equally spaced intervals along the otolith radius. Ralston's method produces an artificially broader and more uniform sample. This is evident in that the one region (NMI) for which the previous estimate was able to converge showed an inadequate fit by the present method, which is consistent with the clustering of data points in the middle of the size range (Fig. 2). Experimental fitting to a Gompertz curve was done initially, but it was found that lack of fit by either method was more attributable to the variance in age estimates and the narrow range of fish sizes than to the choice of a growth curve. The regression of otolith radius on fork length was allometric for all regions examined, so it is not surprising that somatic growth rate is represented as well by the von Bertalanffy curve.

The von Bertalanffy growth constant (K) for the best curves for each region were in the range of 0.129–0.137 for Vanuatu, 0.179–0.310 for NMI, 0.064–0.190 for Hawaii, and 0.039–0.145 for French Polynesia. The highest value of K = 0.464 for NMI, estimated by log-linear regression, was arbitrarily left out of the range for this region as being abnormally high. Any of the estimates for NMI could well be excluded on the basis of the r^2 values. Estimates of natural mortality (M) for these K values using the relationship for snappers and groupers by Ralston (1987) and for various taxa by Ricker (1973) are listed in Table 5. These K estimates agree with those summarized by Manooch (1987) for other species of lutjanids, including several of the subfamily etelinae.

Table 5

Best estimated von Bertalanffy growth constant (K) and corresponding natural mortality estimates by region for the red snapper *Etelis carbunculus*.

	Range of best K estimates	Estimated natural mortality (M)	
		Ralston (1987)*	Ricker (1973)*
Hawaii	0.064–0.190	0.301–0.410	0.279–0.412
Vanuatu	0.129–0.137	0.285–0.301	0.258–0.279
French Polynesia	0.039–0.145	0.099–0.318	0.032–0.299
Northern Marianas	0.179–0.310	0.388–0.658	0.384–0.715

* Sources of regressions used to estimate natural mortality rate (M) from the value of the von Bertalanffy growth constant (K).

Discussion

The method presented is a variation on previous techniques of obtaining age estimates from microincrement densities (Methot 1983, Ralston and Williams 1988a, Gauldie et al. 1989). It provides a direct estimate of the fit of the rate function used to approximate the otolith growth curve, which is then integrated essentially without error. Part of the difficulty in comparing the present age estimates with those of Ralston and Williams was that a direct measure of error was not available for their estimates. Within the constraints of the fit of each rate curve, the present technique provides an accurate estimate of age at any chosen interval of otolith radius. The method also allows age estimation from the otolith focus to its perimeter, where readings become difficult, and gives a reliable estimate of the time transpired between any two points on the otolith radius.

The error introduced in numerical integration by the trapezoid method, dividing the otolith radius into increments of equal length and using the mean growth rate in each interval to estimate age, is well understood (Salas et al. 1986, Atkinson 1989). Most alternative methods of numerical integration have been developed to reduce the error introduced by the trapezoid estimate. Romberg's method is one of the most effective ways of eliminating this error, evaluating and subtracting it out as part of the process of integration. The result is a negligible integration error for the purposes of this discussion. The error in the present method derives from natural variability in otolith growth rates, lack of fit of the chosen rate curve, and any inadequacies in the data. The first two sources of error are measured by the sums of squares, and are represented in the multiple correlation coefficient and asymptotic confidence intervals for parameter estimates. Thus, another advantage of the present method is that alternative curves can be fit to evaluate the advisability of using other functions or combinations of functions to fit the data.

The reliability of these growth estimates is dependent, among other things, upon the assumption that Ralston and Williams were able to count all or most of the increments present in the otoliths at a given radius. This is true to a varying extent; however, the reliability of the readings may decrease as fish get older. Most microincrement density measurements were made within 50–60% of the total otolith radius. However, in each region, there were "legible" segments near the perimeter of some otoliths. The sectioning techniques and optical resolution of the Nikon light microscope and RCA video system used to observe the slides were sufficient to see detail considerably below the scale on which microincrements were recorded. Therefore, we believe that any error in the data is unlikely to have been derived from a failure to observe increments that were present.

Some error in measuring total otolith radius may have occurred, however, due to changes in the orientation of growth along the postrostral axis as fish get larger. Difficulties in reading otolith microincrements in older fish, induced by the transformation in shape and crystalline structure of the otolith affect the legibility of daily increments (Radtke 1987, Davies et al. 1988). Thus an important follow-up to these preliminary estimates is to confirm the orientation of the postrostral growth axis as a function of otolith size for each region. The hypothesis that otolith growth rate is essentially constant beyond a certain radius could be tested by reexamining microincrement densities for some of the larger otoliths near their perimeter.

A difference in actual microincrement densities at maximum otolith radius would influence age estimates significantly. An unmodified Gompertz rate curve (without the constant) was used in early attempts at fitting microincrement densities. This curve fit the data fairly well for small otolith radius, but the decline of the rate curve to zero at greater radius provided a poor fit and caused age estimates for large fish to increase by more than an order of magnitude. A constant was added to the rate curve for these reasons, significantly improving the fit and bringing age estimates into conformity with other estimates by fishery biologists and experienced fishers.

The growth estimates presented can be improved by sampling a wider size range and larger number of organisms and by recording microincrement densities along the full length of the radial axis of all otoliths sampled. For very small fish, increments near the focus can be counted and integration is not necessary to get an age estimate. The size of the sample would be determined by the variance of otolith radius as a function of fork length, a characteristic which varies regionally. Otolith radius, and thus estimated age, was highly variable for a given fork length for all regions for which a sufficiently large sample was available to make this determination. This is evidence that a fairly large sample is necessary in order to have a reliable growth estimate. Sampling a representative number of fish within a full range of sizes and obtaining increment density measurements along the entire otolith radius are important, and should not be done at random.

Despite the utility of the technique of age estimation developed, potential biases in size range and number of otoliths sampled make it difficult to compare growth estimates for *Etelis carbunculus* quantitatively. Results presented imply that a more systematic sampling program may document significant regional differences in growth and population dynamics of this species. The relationship between otolith growth rate and postrostral radius was similar for all regions. However, there were regional differences in the width of otoliths for a given fork length (Appendix 1), wider otoliths being found in Hawaii and French Polynesia. Although there were few fish sampled from Vanuatu and limited overlap occurs with small organisms from the other regions, fish from NMI and Vanuatu had smaller otolith radius (lower estimated age) than fish of similar size from the other two areas. This means that even if growth rates of otoliths were essentially equal throughout the Pacific, fish would be older at a given fork length in Hawaii and French Polynesia. Thus, well below the forced values of asymptotic length used in regressions, regional differences in estimated age are apparent.

Fish apparently grow faster at Vanuatu and NMI than in any of the other regions. However, at NMI they reach less than half the size found in the region near Vanuatu. This suggests there are differences in natural mortality rates for these regions (asymptotic length estimates were obtained from virgin stocks for NMI and in the initial stage of the fishery at Vanuatu). The growth curves for NMI yielded higher estimates of the von Bertalanffy growth constant (K) and, as a result, natural mortality estimates were higher. The differences in K hold true even for the NMI regression that was constrained only in t_0, but as mentioned the results from NMI should be interpreted with caution. Hawaii and French Polynesia showed similar values of K to Vanuatu, but fish from these regions had thicker otoliths and were apparently more slow growing. Possible explanations for such differences include genetic differences in regional stocks, variation in the mean annual temperature, and differences in feeding or food availability.

The estimates of the von Bertalanffy growth curve were in the range of those obtained in previous studies. Although Uchida et al. (1982) estimated K at 0.36 for the Hawaiian Islands, Ralston and Kawamoto (1987) obtained values of 0.15–0.17, which is more consistent with the present results. Both Uchida et al. (1982) and Ralston and Kawamoto (1987) based their estimates on length-frequency data from exploited stocks. Ralston and Williams (1988b) estimated K for virgin stocks at NMI from 0.13 to 0.35, depending on the method used. K estimates from commercial landings data at the onset of the fishery at Vanuatu were in the range 0.07–0.19 (Brouard et al. 1983, Brouard and Grandperrin 1985). Thus, the present K estimates seem reasonable. Estimates of t_0 were considerably greater than zero, except in the case of NMI, which was almost certainly a function of the limited number of small fish included in the data.

The similarity of otolith growth rate at any given radial distance was pointed out by Ralston and Miyamoto (1983), but these authors did not discuss the implications with regard to otolith shape for fish with different growth rates. The similarity of growth rate of otoliths and regional variation in growth rate of fish may explain some regional differences in otolith shape. It also indicates that there are species-specific characteristics of otolith growth from one region to another, as would be expected. If the concept of narrower or thinner otoliths corresponding to faster-growing organisms within a given species can be generally applied to fishes, then this is a tool that can be useful for a number of purposes (for example, in evaluating paleontological evidence of growth rates in sedimentary strata). Although environmental and genetic components of otolith shape must also be considered, differences in growth rate may explain many of the differences in shape which have commonly been used to separate the otoliths of different stocks, or "races," of the same species (Postuma and Zijlstra 1958, Parrish and Sharman 1959, Kotthaus 1961, Messieh 1972, Bird et al. 1986). Variation in growth may also explain sex-linked differences in the thickness of otoliths of sexually dimorphic fishes (Gaemers and Crapon de Crapona 1986). The present study is a contribution to the development of methodology that will be useful in evaluating these and other questions regarding the growth rate and shape of otoliths.

Acknowledgments

We thank Steve Ralston and Happy Williams for their cooperation throughout this study, their constructive suggestions, and for making the data and a detailed explanation of their methods available. Data were collected and compiled by Ralston and Williams with the collaboration of Rene Grandperrin of the Noumea Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM), and Louise Wrobel of the Etablissement pour la Valorisation des Activites Aquacoles et Maritimes (EVAAM, French Polynesian Ministerie de la Mer). We also thank Robert Gauldie, Jeff Polovina and George Boehlert for critical review of the manuscript. This research was conducted while the senior author held a National Research Council Postdoctoral Associateship, through the funding of the National Marine Fisheries Service Southwest Fisheries Center, Honolulu Laboratory.

Citations

Atkinson, K.E.
1989 An introduction to numerical analysis. John Wiley, NY, 693 p.

Barkman, R.C.
1978 The use of otolith growth rings to age young Atlantic silversides, *Menidia menidia*. Trans. Am. Fish. Soc. 107(6): 790–792.

Bird, J.L., D.T. Eppler, and D.M. Checkley Jr.
1986 Comparison of herring otoliths using Fourier series shape analysis. Can. J. Fish. Aquat. Sci. 43:1228–1234.

Brothers, E.B., C.P. Mathews, and R. Lasker
1976 Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1–8.

Brouard, F., and R. Grandperrin
1985 Deep-bottom fishes of the outer reef slope in Vanuatu. *In* 17th Regional Technical Meeting on Fisheries, South Pacific Comm., ORSTOM, New Caledonia, [Engl. transl.], 127 p.

Brouard, F., R. Grandperrin, M. Kulbicki, and J. Rivaton
1983 Note on readings of daily increments observed on the otoliths of deepwater demersal fishes at Vanuatu. ORSTOM Notes et Documents d'Oceanographie 8, 9 p. [Transl. 88, W.G. Van Campen, avail. Honolulu Lab., NMFS, Southwest Fish. Sci. Cent.]

Carlot, A.H., and F. Nguyen
1989 Preliminary study on population dynamics of Vanuatu deep bottom fish after seven years of exploitation,. Paper presented at Tropical Fisheries Resource Assessment Workshop, sponsored by US AID–National Marine Fisheries Service–University of Hawaii, Manoa, July 5–26, 1989, 23 p. Avail. Fish. Dep., Port Vila, Vanuatu.

Davies, N.M., R.W. Gauldie, S.A. Crane, and R.K. Thompson
1988 Otolith ultrastructure of smooth oreo, *Pseudocyttus maculatus*, and black oreo, *Allocyttus* sp., species. Fish. Bull., U.S. 86:499–515.

Davis, P., and P. Rabinowitz
1984 Methods of numerical integration, 2d ed. Academic Press, NY, 612 p.

Gaemers, P.A.M., and M.D. Crapon de Crapona
1986 Sexual dimorphism in otoliths of haplochromines (Pisces, Cichlidae). Ann. Mus. R. Afr. Cent. Sc. Zool. 251:151–155.

Gaschütz, G., D. Pauly, and N. David
1988 A versatile BASIC program for fitting weight and seasonally oscillating length growth data. Int. Counc. Explor. Sea, CM 1980/D:6 Statistics Committee, 23 p.

Gauldie, R.W., I.F. West, and N.M. Davies
1989 K-selection characteristics of orange roughy (*Hoplostethus atlanticus*) stocks in New Zealand waters. J. Appl. Ichthyol. 5:127–140.

Geffen, A.J.
1986 The growth of herring larvae, *Clupea harengus* L., in the Clyde: An assessment of the suitability of otolith ageing methods. J. Fish Biol. 28:279–288.

Gompertz, B.
1825 On the nature of the function expressive of the law of human mortality, and on a new method of determining the value of life contingencies. Philos. Trans. R. Soc. Lond. 513–585.

Jones, C.
1986 Determining age of larval fish with the otolith increment technique. Fish. Bull., U.S. 84:91–103.

Jones, C., and E.B. Brothers
1987 Validation of the otolith increment ageing technique for striped bass, *Morone saxatilis*, larvae reared under suboptimal feeding conditions. Fish. Bull., U.S. 85:171–178.

Kotthaus, A.
1961 Preliminary remarks about redfish otoliths. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 150:45–50.

Manooch, C.S. III
1987 Age and growth of snappers and groupers. *In* Polovina, J.J., and S. Ralston (eds.), Tropical snappers and groupers: Biology and fisheries management, p. 329–373. Westview Press, Boulder, CO.

McGurk, M.D.
1984 Ring deposition in the otoliths of larval Pacific herring *Clupea harengus pallasi*. Fish. Bull., U.S. 82:113–120.

Messieh, S.N.
1972 Use of otoliths in identifying herring stocks in the southern Gulf of St. Lawrence and adjacent waters. J. Fish. Res. Board Can. 29:1113–1118.

Methot, R.D. Jr.
1981 Spatial covariation of daily growth rates of larval northern anchovy, *Engraulis mordax*, and the northern lampfish, *Stenobrachius leucopsarus*. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 178:424–431.
1983 Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. Fish. Bull., U.S. 81:741–750.

Neilson, J.D., G.H. Geen, and D. Bottom
1985 Estuarine growth of of juvenile chinook salmon (*Oncorhynchus tshawytcha*) as inferred from otolith microstructure. Can. J. Fish. Aquat. Sci. 42:899–909.

Pannella, G.
1971 Fish otoliths: Daily growth layers and periodical patterns. Science (Wash. DC) 173:1124–1127.
1974 Otolith growth patterns: An aid in age determination in temperate and tropical fishes. *In* Bagenal, T.B. (ed.), The ageing of fish, p. 28–39. Unwin Bros., Surrey, England.

Parrish, B.B., and D.P. Sharman
1959 Otolith types among summer-autumn spawning herring in the Northern North Sea. J. Cons. Perm. Int. Explor. Mer 25:81–92.

Postuma, K.H., and J.J. Zijlstra
1958 On the distinction between herring races in autumn and winter spawners in the North Sea and English Channel by means of otoliths and the application of this method in tracing offspring of races along the continental coast. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 143(2):130-133.

Radtke, R.L.
1987 Age and growth information available from the otoliths of the Hawaiian snapper, *Pristipomoides filamentosus*. Coral Reefs 6:19-25.

Ralston, S.
1976 Age determination of a tropical reef butterflyfish utilizing daily growth rings of otoliths. Fish. Bull., U.S. 74: 990-994.
1981 A study of the Hawaiian deepsea handline fishery with special reference to the population dynamics of opakapaka, *Pristipomoides filamentosus* (Pisces: Lutjanidae). Doctoral diss., Coll. Fish., Univ. Wash., Seattle, 204 p.
1985 A novel approach to aging tropical fish. ICLARM (Int. Cent. Living Aquat. Resour. Manage.) Newsletter 8(1):14-15.
1987 Mortality rates of snappers and groupers. *In* Polovina, J.J., and S. Ralston (eds.), Tropical snappers and groupers: Biology and fisheries management, p. 375-404. Westview Press, Boulder, CO.

Ralston, S., and K. Kawamoto
1987 An assessment and description of the status of bottom fish stocks in Hawaii. Admin. Rep. H-87-7, NMFS Southwest Fish. Sci. Cent., Tiburon, CA, 55 p.

Ralston, S., and G.T. Miyamoto
1981 Estimation of the age of a tropical reef fish using the density of daily growth increments. *In* Gomez, E.D., et al. (eds.), The reef and man; Proc., 4th Int. Coral Reef Symp., Mar. Sci Cent., Univ. Philippines, Manila, vol. 1, p. 83-88.
1983 Analyzing the width of daily otolith increments to age the Hawaiian snapper, *Pristipomoides filamentosus*. Fish. Bull., U.S. 81:523-535.

Ralston, S., and H.A. Williams
1988a Numerical integration of daily growth increments: An efficient means of ageing tropical fishes for stock assessment. Fish. Bull., U.S. 87:1-16.
1988b Depth distributions, growth, and mortality of deep slope fishes from the Mariana Archipelago. U.S. NOAA-TM-NMFS-SWFC Tech. Memo. 113, NMFS Southwest Fish. Sci. Cent., Tiburon, CA, 47 p.

Ricker, W.E.
1973 Linear regressions in fishery. J. Fish. Res. Board Can. 30:409-434.

Salas, S.L., E. Hille, and J.T. Anderson
1986 Calculus, 5th ed. John Wiley, NY, 719 p.

SAS (Statistical Analysis System)
1985 Version 6. A series of user's manuals, statistical procedures and software for the personal computer. SAS Inst. Inc., Cary, NC.

Struhsaker, P., and J.H. Uchiyama
1976 Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74:9-17.

Uchida, R.N., D.T. Tagami, and J.H. Uchiyama
1982 Results of bottom fish research in the northwestern Hawaiian Islands. Admin Rep. H-82-10, Honolulu Lab., Southwest Fish. Sci. Cent., 15 p.

von Bertalanffy, L.
1957 Quantitative laws in metabolism and growth. Q. Rev. Biol. 32:217-231.

Wall, H.S.
1948 Analytic theory of continued fractions. D. Van Nostrand, NY, 433 p.

Wild, A., and T.J. Foreman
1980 The relationship between otolith increments and time for yellowfin and skipjack tuna marked with tetracycline. Inter-Am. Trop. Tuna Comm. Bull. 17:557-590.

Winsor, C.P.
1932 The Gompertz curve as a growth curve. Proc. Natl. Acad. Sci. 18(1):1-8.

Wrobel, L.
1985 La peche profonde en Polynesie Francaise. Etablissement pour la valorisation des activites aquacoles et maritimes (EVAAM), Minist. de la Mer, French Polynesia, 81 p.