

Regional Differences in Otolith Morphology of the Deep Slope Red Snapper *Etelis carbunculus*

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Sagittal otoliths from four populations of the Pacific deep slope red snapper *Etelis carbunculus* Cuvier were compared using Fourier descriptors and other shape indices, linear proportions, and dry weight. Otoliths from Hawaii, Vanuatu, Fiji and French Polynesia and a small number from the Commonwealth of the Northern Marianas Islands (NMI) were examined. Regional shape and weight characteristics were distinguishable, despite the wide range of individual variation and limited available size range from some regions. Size-specific differences in otolith shape were found for the four regions for which a sufficient sample was available. Otoliths from Hawaii, French Polynesia, and NMI showed a significant shape affinity. Otoliths from Fiji and Vanuatu were similarly shaped and were distinct from those from the other three regions. Interregional otolith shape affinities for the stocks examined parallel similarities in maximum size and growth rate from the literature, suggesting that growth rate may influence otolith shape. Observed trends in otolith weight as a function of fish length support growth-related regional differences in otolith shape.

Des otolithes sagittaux de quatre populations de vivanneaux du Pacifique (*Etelis carbunculus* Cuvier) ont été comparés à l'aide de descripteurs de Fourier et d'autres indices de taille, des proportions linéaires et du poids sec. Des otolithes provenant d'Hawaï, du Vanuatu, des Fidji et de la Polynésie française et un petit nombre du Commonwealth des îles Mariannes du Nord (IMN) ont été examinés. On pouvait distinguer des caractéristiques régionales de forme et de poids, en dépit de la grande diversité de variations individuelles et de la plage limitée des tailles disponibles pour certaines régions. On a observé les différences propres à l'espèce dans la forme des otolithes dans quatre régions pour lesquelles un échantillon suffisant était disponible. Les otolithes d'Hawaï, de la Polynésie française et des IMN présentaient une affinité de forme significative, alors que les otolithes des Fidji et de Vanuatu avaient des formes semblables et étaient distinctes de celles des trois autres régions. Les profils des affinités interrégionales des formes d'otolithes des stocks examinés sont semblables aux ressemblances des tailles maximum et des taux de croissance mentionnées dans la documentation, ce qui suggère que le taux de croissance peut influencer la forme des otolithes. Les tendances observées du poids des otolithes en fonction de la longueur du poisson appuient l'hypothèse des différences régionales en rapport avec la croissance pour expliquer la forme des otolithes.

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The ehu (*Etelis carbunculus*) is a red snapper of the family Lutjanidae. The Etelinae, one of the four subfamilies of Lutjanidae, comprise five genera: *Aphareus*, *Aprion*, *Etelis*, *Pristipomoides*, and *Randallichthys*. *Etelis carbunculus* are captured from the coast of Africa as far east as Hawaii and French Polynesia, as summarized by Allen (1985). They represent one of the principal species in the commercial hand-line catch from steep, rocky slopes at depths of 200-450 m.

Throughout the Pacific, *Etelis carbunculus* Cuvier (in Cuvier and Valenciennes 1828) has been referred to as *Etelis marshi*. Both Fourmanoir (1971) and Anderson (1981) pointed out that there were no significant morphological differences between specimens collected in the Pacific and those from the Seychelles Archipelago, previously described as *Etelis carbunculus*. Anderson's (1981) clarification of the morphological distinctions between *Etelis coruscans* and *Etelis carbunculus* further reduced confusion regarding the

geographic distribution and taxonomy of these two snappers. However, significant questions remain regarding the remarkable differences in the maximum size reached by *Etelis carbunculus* in different areas of the Pacific.

Fishermen and fisheries biologists have brought to light differences of over 50 cm in the maximum size of ehu captured in various regions of the northern and southern tropical Pacific. Fish measuring up to 90-110 cm (fork length) are found between the Cook Islands, Papua New Guinea, and the northeast coast of Australia (Brouard and Grandperrin 1985; Schaan et al. 1987; Lewis et al. 1988; Carlot and Nguyen 1989; Latu and Tulua;² Lokani et al.³; Nath and

²T. F. Latu and S. Tulua. Estimated maximum sustainable yield for Tonga deep bottom fishery. Contrib. Minist. Agric., Fish. and For., Fish. Div., Kingdom of Tonga, USAID Trop. Fish. Res. Assess. Workshop, July 1989, Honolulu, HI. 15 p. (Manuscr.)

³P. Lokani, H. Pili, and G. Tiroba. Assessment of bottomfish resources of Papua New Guinea. USAID Trop. Fish. Res. Assess. Workshop, July 1989, Honolulu, HI. 13 p. (Manuscr.)

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Sesewa⁴; Sua⁵). The largest fish reported in this region, at Vanuatu, weighed 12.2 kg and is estimated to have measured 127 cm (R. Grandperrin, ORSTOM, Centre de Noumea, Boite Postale A5, Noumea Cédex, Nouvelle Calédonie, pers. comm.). Maximum fish sizes for Hawaii and French Polynesia and in the range of 65–75 cm (Uchiyama and Tagami 1984; Wrobel 1985; Ralston and Kawamoto 1987), while ehu as large as 58 cm are rarely found in the region surrounding the Commonwealth of the Northern Marianas Islands (NMI) (Ralston and Williams 1988). Regional differences in maximum size between these stocks are evidence of their relative isolation, probably maintained by the distances and depths that separate them.

This study describes regional differences in otolith morphology in five areas of the Pacific. It began as an effort to evaluate the reasons for differences in maximum size. Regional otolith shape differences were so remarkable that they were first believed to be an indication of taxonomic differences between stocks. However, examination of regional specimens confirmed that all were *Etelis carbunculus*.

Materials and Methods

Fork lengths were recorded and sagittal otoliths collected from *Etelis carbunculus* captured at five sites throughout the Pacific between 100 and 400 m of depth. Otoliths were washed in 70% alcohol, dried, and stored in plastic envelopes. Following the measurements described below, sagittae were oven-dried and desiccated to a constant weight. A resin cast of the saccular lumen was made for a few fish of each size from Hawaii. Otoliths collected on a regional basis are summarized below:

Region	Year(s)	No. of otolith Pairs
Hawaiian Islands	1989	130
	1987	26
Fijian Islands	1989	109
	1985–86	42
French Polynesia	1989	32
	1982	6
NMI	1989	6
	1983	84

The growth focus is a useful point of reference, visible from the unsectioned otolith's concave lateral side. The view of the otolith from this side is referred to herein as the "lateral view" (see Fig. 1). To make the focus more apparent, otoliths were cleared using a glycerine and alcohol (2:3) mixture. The following proportions (Fig. 1) were recorded through a dissecting microscope from the video-relayed image (lateral view) of one of each pair of otoliths, using an optical software system designed by Biosonics, Inc. (1987): (1) distance from tip of rostrum to focus, (2) distance from postrostrum to focus, (3) distance from sulcus groove to tip of rostrum, (4) dorsal (i) and ventral (ii) width at the focus, (5) length from postrostrum to sulcus, (6) length from sulcus to tip of antirostrum, and (7) basal width of antirostrum.

⁴G. Nath and A. Sesewa. Progress report on fisheries research conducted on bottomfish stocks around the Fijian Republic. Contrib. Fish. Div., Minist. Primary Ind., Republic of Fiji, USAID Trop. Fish. Res. Assess. Workshop, July 1989, Honolulu, HI. 21 p. (Manuscr.)

⁵T. Sua. Assessment of bottomfish resources of Western Samoa: an interim report. USAID Trop. Fish. Res. Assess. Workshop, July 1989, Honolulu, HI. 20 p. (Manuscr.)

Otoliths were immobilized parallel to the field of view on a stand of polyurethane foam. The perimeter of each otolith was traced in a counterclockwise direction from two different perspectives, the ventral and lateral views. Each outline was digitized into a set of 128 virtual x, y coordinates, taken at equally spaced intervals along its perimeter, and a Fast Fourier Transform (FFT) of these points was taken of the form

$$(1) R(\Theta) = A_0 + \sum_{n=1}^{128} A_n \cos(\Theta_n + \phi_n)$$

where the original particle representation and angular position ($R(\Theta)$) are decomposed into a standardized starting position (A_0) and 128 consecutive amplitude coefficients (A_n), with angular components (Θ_n) and slope components (ϕ_n). Rotational and size invariance was achieved by (1) dividing the amplitude coefficients by the amplitude of the first descriptor (A_1), (2) setting the A_0 frequency component to zero, and (3) iteratively rotating the shape in the frequency domain until an optimization function was maximized. The technique is outlined briefly in the Biosonics, Inc. (1987) manual and in more detail in references dealing with shape analysis (Alt 1962; Hu 1962; Clark 1981).

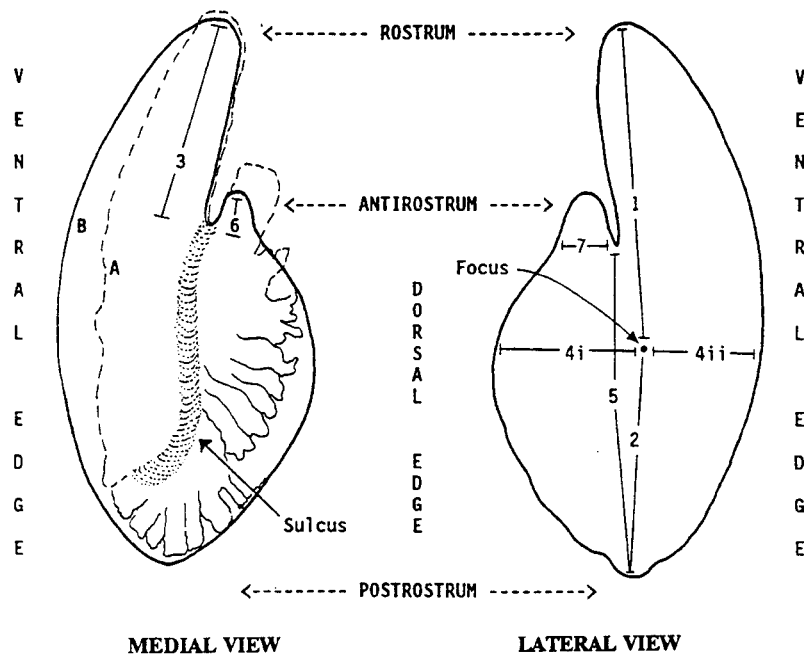
While the video-flattened lateral and ventral images made shape comparisons essentially two-dimensional, the ventral view provided an index of otolith curvature and the lateral silhouette showed much of the variation in overall shape. Two other characteristics recorded from the lateral view were the indices of (1) circularity, the perimeter squared divided by the area, and (2) rectangularity, the shape's area divided by the area of its minimum enclosing rectangle. Normalized Fourier descriptors, scaled indices of rectangularity and circularity, and ratios of linear proportions provided size-independent indices of otolith shape, allowing comparison of different sized otoliths.

The first 20 amplitudes ("harmonics") after A_0 and A_1 were used to characterize each FFT (normalization functions set $A_0 = 0$ and $A_1 = \text{unity}$ for all FFTs). The amplitude of each harmonic (A_n of equation 1) was calculated from Biosonics sine and cosine output (Castonguay et al. 1991) according to the relationship (Christopher and Waters 1974)

$$(2) A_n = \sqrt{\sin_n^2 + \cos_n^2}$$

To evaluate whether otolith shape indices and weights varied as a function of fish size, otoliths were grouped by 10-cm fork length intervals and the indices were compared between size groups and regions using a Student–Newman–Keuls (SNK) means test (Sokal and Rohlf 1969). Regional nonhierarchical cluster analyses of linear proportions, harmonics, and shape indices were performed by the SAS "Fastclus" procedure (SAS Institute Inc. 1985), which clusters data into discrete groups by nearest centroid sorting using a k -means method (Anderberg 1973) on squared Euclidean distances (referred to hereinafter as NC cluster analysis).

Linear combinations of the multivariate regional shape characteristics were compared by canonical discriminant analyses (SAS "Candisc" procedure). The first and second canonical variables are maximally uncorrelated descriptors of the first- and second-order multiple regressions, respectively, used to characterize the sample in two dimensions. Interregional groupings were also evaluated using hierarchical average linkage cluster analyses (SAS "Cluster" procedure) on squared Euclidean distances. To avoid the disproportionate weighting of measurements made in different units or showing a wider range of variation, all cluster analyses were performed on data mat-



GENERAL SHAPE SHOWN FOR THE FOLLOWING REGIONS
(MEDIAL VIEW)

<p>A Fiji/Vanuatu</p> <p>B Hawaii/NMI/French Polynesia</p>	<p>Symbol</p> <p>----- (dashed line)</p> <p>———— (solid line)</p>
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FIG. 1. Medial and lateral views of the right sagittal otolith of the deep slope snapper (*Etelis carbunculus*).

rices standardized to dimensionless units with mean zero and standard deviation unity (Romesburg 1984).

Results

Dissection of fish skulls showed that the otolith abuts against the ventral and medial wall of each otic capsule (sacculus). Both the dorsal edge and outer lateral surface of the otolith are unconstrained by the bony walls of the otic capsule, extending into the macular lumen and held in place only by a gelatinous material. Resin casts of the saccular lumen for fish from Hawaii produced a mold almost identical to the ventral and medial surfaces of the otolith, while the casts were 4–6 times as thick and concave rather than convex like the otolith on their outer surface. Otoliths of small fish (<30 cm fork length) had some space within the otic capsule, even along the medial surface, while otoliths of medium-sized (30–50 cm) and large (>50 cm) fish fit more and more snugly into the sacculus, their shape increasingly molded to that of the ventral and medial surfaces of the otic capsule. The constraints on otolith shape imposed by the chamber that contains them may account for

much of the curvature and uniqueness of form which develops in the otoliths of large fish.

The relationship between fork length and linear otolith dimensions was examined by log-linear regression (Table 1). Although results obtained by this method are affected by the size range included in each regression, they are mentioned because of the interesting variation observed for all regions. Regression parameters for all six linear proportions (illustrated in Fig. 1) were allometric (*b* always less than 1) and varied in a regional and character-specific manner. While differences between regional samples are to be expected for several reasons, within-region variation in otolith growth rate along different axes (evidenced by within-region variation in *b* values) and in individual variability of these traits for the same otoliths (indicated by varying coefficients of determination, *r*²) illustrates the complex three-dimensional nature of otolith growth. Regional regression parameters for otolith weight versus fork length are included in Table 1, along with predicted values of otolith weight within an intermediate fork length range, for the four regions that were well represented numerically. Predicted weight for Vanuatu was the lowest, followed in increasing order by Fiji, Hawaii, and French Polynesia.

TABLE 1. Allometric relationships for fork length versus otolith weights and linear dimensions.

Region	Otolith weight/ linear dimension	<i>a</i>	<i>b</i>	<i>n</i>	<i>r</i> ²
Hawaii	Otolith weight	4.383 × 10 ⁻⁶	1.66	106	0.9512
	Rostral radius	222.2	0.56	128	0.7605
	Postrostral radius	165.6	0.58	128	0.8323
	Total length (at focus)	387.9	0.57	128	0.8949
	Dorsal radius	140.2	0.52	128	0.8134
	Total width (at focus)	217.4	0.55	128	0.8798
	Postrostrum-sulcus length	479.3	0.48	128	0.8573
NMI	Otolith weight	3.038 × 10 ⁻⁶	1.74	9	0.8611
	Rostral radius	65.1	0.78	12	0.8193
	Postrostral radius	282.1	0.50	12	0.8511
	Total length (at focus)	255.6	0.65	12	0.8578
	Dorsal radius	443.4	0.32	12	0.3419
	Total width (at focus)	417.9	0.44	12	0.6415
	Postrostrum-sulcus length	388.1	0.52	12	0.7647
French Polynesia	Otolith weight	4.193 × 10 ⁻⁷	2.10	67	0.9038
	Rostral radius	40.6	0.86	69	0.8464
	Postrostral radius	132.3	0.63	69	0.6510
	Total length (at focus)	138.2	0.76	69	0.8713
	Dorsal radius	80.0	0.63	69	0.6517
	Total width (at focus)	146.7	0.62	69	0.7608
	Postrostrum-sulcus length	477.3	0.49	69	0.7467
Fiji	Otolith weight	3.784 × 10 ⁻⁷	2.017	105	0.8250
	Rostral radius	110.9	0.68	108	0.7774
	Postrostral radius	70.0	0.73	108	0.7510
	Total length (at focus)	179.2	0.70	108	0.8264
	Dorsal radius	88.6	0.58	108	0.4880
	Total width (at focus)	227.6	0.52	108	0.6381
	Postrostrum-Sulcus length	278.0	0.58	108	0.6921
Vanuatu	Otolith weight	5.164 × 10 ⁻⁶	1.60	82	0.8859
	Rostral radius	204.1	0.59	84	0.8718
	Postrostral radius	101.7	0.70	84	0.8895
	Total length (at focus)	295.7	0.63	84	0.9158
	Dorsal radius	188.3	0.48	84	0.7345
	Total width (at focus)	332.9	0.47	84	0.8081
	Postrostrum-sulcus length	449.3	0.51	84	0.8682

Equation: $y = ax^b$ where $x =$ fork length (mm) and $y =$ linear dimension (μm) or dry weight (g)

Fork length (mm)	Predicted otolith weight (g)			
	Fiji	Vanuatu	Hawaii	French Polynesia
300	0.038	0.048	0.057	0.063
400	0.067	0.077	0.092	0.114
500	0.105	0.110	0.133	0.182
600	0.152	0.147	0.180	0.267
700	0.208	0.188	0.233	0.368

Regional differences in otolith morphology are a complex topic, since otoliths from all regions (except NMI for which the size range and number of samples were too small) showed significant differences in shape as a function of size. Table 2 summarizes the results of SNK means comparisons for each region for indices of otolith circularity and rectangularity. A circle would have the minimum circularity value ($4\pi = 12.57$), while a rectangle (or square) would have the maximum rectangularity value (unity). Tabled values indicate that large otoliths from all regions were both less circular and less rectangular than smaller ones. In some cases, decreasing circularity or rectangularity was apparent, but not statistically significant, due to a high sample-wide variability in shape and/or a small number of samples in some size groups. It is worth noting that the indices of circularity and rectangularity are not inverses, since

a circle and a square (or rectangle) have some symmetrical similarities. Furthermore, a shape's departure from rectangularity or circularity varies in two dimensions, while the numerical values of both shape indices vary linearly. This influences each index somewhat differently. Having an equal and larger number of otoliths from each size group would have helped clarify size-related shape differences, but the constraints of fishing and sampling opportunities worked out through cooperative long-distance agreements made this optimum difficult to achieve.

The ratios of linear measurements (Table 3) provided a good index of regional otolith shape variation. Data were pooled irrespective of size because they showed the same regional groupings (SNK, $\alpha \leq 0.01$), regardless of whether they were segregated by size. Regional groupings were similar to those seen for indices of circularity and rectangularity. The long and nar-

TABLE 2. Results of SNK means comparisons ($\alpha = 0.01$) for average otolith circularity and rectangularity as a function of size group by 10-cm intervals of fork length. Underlined values are not significantly different.

Region/characteristic	Length group (cm)					
	<30	31-40	41-50	51-60	61-70	71-80 >80
Mean circularity						
Hawaii	23.45	<u>27.06</u>	<u>28.64</u>	31.13	31.28	(more circular)
French Polynesia	<u>24.24</u>	<u>25.74</u>	<u>28.53</u>	36.08		
Fiji			<u>31.94</u>	<u>35.28</u>	38.80	<u>45.87</u> <u>46.71</u>
Vanuatu	<u>29.30</u>	<u>29.00</u>	<u>33.89</u>	<u>33.86</u>	<u>39.75</u>	<u>45.47</u> <u>42.98</u>
NMI	<u>26.32</u>	<u>27.97</u>	<u>29.97</u>			
Mean rectangularity						
Hawaii	<u>0.6372</u>	<u>0.6202</u>	<u>0.6064</u>	<u>0.5966</u>	0.5381	(more rectangular)
French Polynesia	<u>0.6453</u>	<u>0.6207</u>	<u>0.6122</u>	<u>0.5850</u>		
Fiji			0.5726	0.5251	0.5044	0.4999 0.4865
Vanuatu	<u>0.6003</u>	<u>0.5940</u>	<u>0.5369</u>	<u>0.5304</u>	<80 0.5238	61-70 0.4924 71-80 0.4791
NMI	<u>0.6455</u>	<u>0.6468</u>	<u>0.6439</u>			
Number of otoliths per size group						
Hawaii	42	28	37	11	1	
French Polynesia	17	40	10	2		
Fiji			8	35	33	19 13
Vanuatu	4	11	12	8	19	23 7
NMI	5	5	2			

TABLE 3. Results of SNK comparisons ($\alpha = 0.05$) between mean ratios of linear otolith measurements. Underlined values are not significantly different.

Ratios of otolith linear measurements	Regional mean (%)				
	Fiji	Vanuatu	NMI	Hawaii	French Polynesia
Rostral radius/ Total length	52.47	<u>53.76</u>	<u>54.10</u>	54.18	<u>54.76</u>
Postrostral radius/ total length	47.53	<u>46.24</u>	<u>45.90</u>	45.82	<u>45.24</u>
Postrostral radius/ postrostrum-sulcus length	67.59	65.48	<u>63.45</u>	<u>62.75</u>	<u>61.63</u>
Total width/total length	39.65	41.66	<u>50.21</u>	<u>49.55</u>	<u>49.39</u>
Total width/ postrostrum-sulcus length	56.42	58.88	<u>69.47</u>	<u>67.92</u>	<u>67.27</u>
Dorsal width/ postrostrum-sulcus length	31.98	34.48	<u>37.59</u>	<u>37.36</u>	<u>37.00</u>
n for all tests	108	84	12	128	69

row otoliths from Fiji and Vanuatu segregated from those from the other regions, except for two instances where Vanuatu was grouped with the other three locations. Otoliths from Fiji and Vanuatu were significantly different for these proportions, while those from French Polynesia, Hawaii, and NMI could not be distinguished statistically.

Using the same six linear ratios and a seventh character, the ratio of the length from focus to tip of rostrum to that from postrostrum to sulcus (1:5 from Fig. 1), NC cluster analysis produced similar regional groupings (Table 4). The five-cluster-level partitioning of regional samples can be compared visually (table percentages in the last row of each section). Hawaiian and French Polynesian samples were primarily

represented in clusters 1 and 3 whereas otoliths from Fiji and Vanuatu were more abundant in clusters 4 and 5. The sample size for NMI was very small, but these otoliths were mostly grouped into clusters 1 and 3 with those from Hawaii and French Polynesia.

The A_{2-22} harmonics (ventral and lateral views) formed similar regional NC clusters (Table 5). Since the results were consistent, regardless of size category, data were again pooled. Whatever index of shape was chosen, otoliths from Fiji and Vanuatu were segregated from those from Hawaii, French Polynesia, and NMI. As might be expected, FFT shapes produced more discrete clusters than linear proportions, and these were more well defined for the lateral than for the ventral view.

TABLE 4. Regional nearest centroids clusters of the ratios of seven otolith traits for deep slope red snapper. Data presented as frequency, overall %, row %, and column %.

Cluster	Region					No. per cluster and %
	Fiji	Hawaii	NMI	French Polynesia	Vanuatu	
1	1	71	6	35	6	119
	0.25	17.71	1.50	8.73	1.50	29.68
	0.84	59.66	5.04	29.41	5.04	
2	0.93	55.47	50.00	50.72	7.14	
	6	3		2	3	14
	1.50	0.75		0.50	0.75	3.49
3	42.86	21.43		14.29	21.43	
	5.56	2.34		2.90	3.57	
	3	37	4	20	2	66
4	0.75	9.23	1.00	4.99	0.50	16.46
	4.55	56.06	6.06	30.30	3.03	
	2.78	28.91	33.33	28.99	2.38	
5	48	2	1		20	71
	11.97	0.50	0.25		4.99	17.71
	67.61	2.82	1.41		28.17	
6	44.44	1.56	8.33		23.81	
	50	15	1	12	53	131
	12.47	3.74	0.25	2.99	13.22	32.67
7	38.17	11.45	0.76	9.16	40.46	
	46.30	11.72	8.33	17.39	63.10	
	Total n	108	128	12	69	84
%	26.93	31.92	2.99	17.21	20.95	100.00

Pseudo *F* statistic = 151.8

$\chi^2_{df 24, P < 0.0001} = 632.9$

Ratios of otolith linear proportions	Corresponding numerical references from Fig. 1
Rostral radius/total length	1:(1 + 2)
Rostral radius/postrostrum-sulcus length	1:5
Postrostral radius/total length	2:(1 + 2)
Postrostral radius/postrostrum-sulcus length	2:5
Total width/total length	(4i + 4ii):(1 + 2)
Total width/postrostrum-sulcus length	(4i + 4ii):5
Dorsal width/postrostrum-sulcus length	4i:5

Canonical discriminant analyses (CDA) and hierarchical clustering were designed to evaluate between-region shape affinities. CDA were used to represent multidimensional shape vectors in a single plane, allowing both quantitative and qualitative assessment of the proximity and content of specific clusters. Plots of canonical discriminant functions from both types of shape indices (Fig. 2) show two principal clusters connected by a transition zone. The cluster group nearest the origin and the y-axis primarily contains otoliths from Hawaii and French Polynesia (with a few from NMI). The transition zone and the cluster closer to the upper range of the x-axis (and widely dispersed along the y-axis) are mainly composed of otoliths from Fiji and Vanuatu. The results are shown for six linear dimensions, circularity, and rectangularity (Fig. 2A) and for the first 10 harmonic descriptors (Fig. 2B, lateral view).

Using regional mean values for the three sets of traits listed in Tables 4 and 5, hierarchical cluster analyses linked otolith shapes from French Polynesia, NMI, and Hawaii and distinguished them from those from Vanuatu and Fiji (Fig. 3). FFT data show a greater definition between regions, since harmonics represent a more sensitive shape indicator.

TABLE 5. Regional groups by nearest centroid clustering of 20 otolith FFT harmonic amplitudes (A_{2-22}). Data presented as frequency, overall %, row %, and column %.

Cluster	Region					No. per cluster and %
	Fiji	Hawaii	NMI	French Polynesia	Vanuatu	
<i>Lateral view</i>						
1	5				3	8
	1.32				0.79	2.11
	62.50				37.50	
2	4.85				3.16	
	21				20	41
	5.53				5.26	10.79
3	51.22				48.78	
	20.39				21.05	
	56	24	2	5	44	131
4	14.74	6.32	0.53	1.32	11.58	34.47
	42.75	18.32	1.53	3.82	33.59	
	54.37	18.60	16.67	12.20	46.32	
5	12				7	19
	3.16				1.84	5.00
	63.16				36.84	
6	11.65				7.37	
	9	105	10	36	21	181
	2.37	27.63	2.63	9.47	5.53	47.63
7	4.97	58.01	5.52	19.89	11.60	
	8.74	81.40	83.33	87.80	22.11	
	Total n	103	129	12	41	95
%	27.11	33.95	3.16	10.79	25.00	100.00

Pseudo *F* statistic = 201.9

$\chi^2_{df 24, P < 0.0001} = 778.5$

Cluster	Region					No. per cluster and %
	Fiji	Hawaii	NMI	French Polynesia	Vanuatu	
<i>Ventral view</i>						
1	35	9	1	2	28	75
	9.19	2.36	0.26	0.52	7.35	19.69
	46.67	12.00	1.33	2.67	37.33	
2	33.65	7.03	8.33	4.76	29.47	
	1				1	0.26
	0.26				10.000	
3	0.78				4	6
	1.05			2	0.52	1.57
	66.67			33.33		
4	3.12			4.76		
	63	44	3	9	58	177
	16.54	11.55	0.79	2.36	15.22	46.46
5	35.59	24.86	1.69	5.08	32.77	
	60.58	34.38	25.00	21.43	61.05	
	6	70	8	29	9	122
6	1.57	18.37	2.10	7.61	2.36	32.02
	4.92	57.38	6.56	23.77	7.38	
	5.77	54.69	66.67	69.05	9.47	
Total n	104	128	12	42	95	381
%	27.30	33.60	3.15	11.02	24.93	100.00

Pseudo *F* statistic = 250.4

$\chi^2_{df 24, P < 0.0001} = 653.9$

Discussion

This study summarizes evidence of regional and local variation in morphology of the otoliths of *Etelis carbunculus*. Rapid

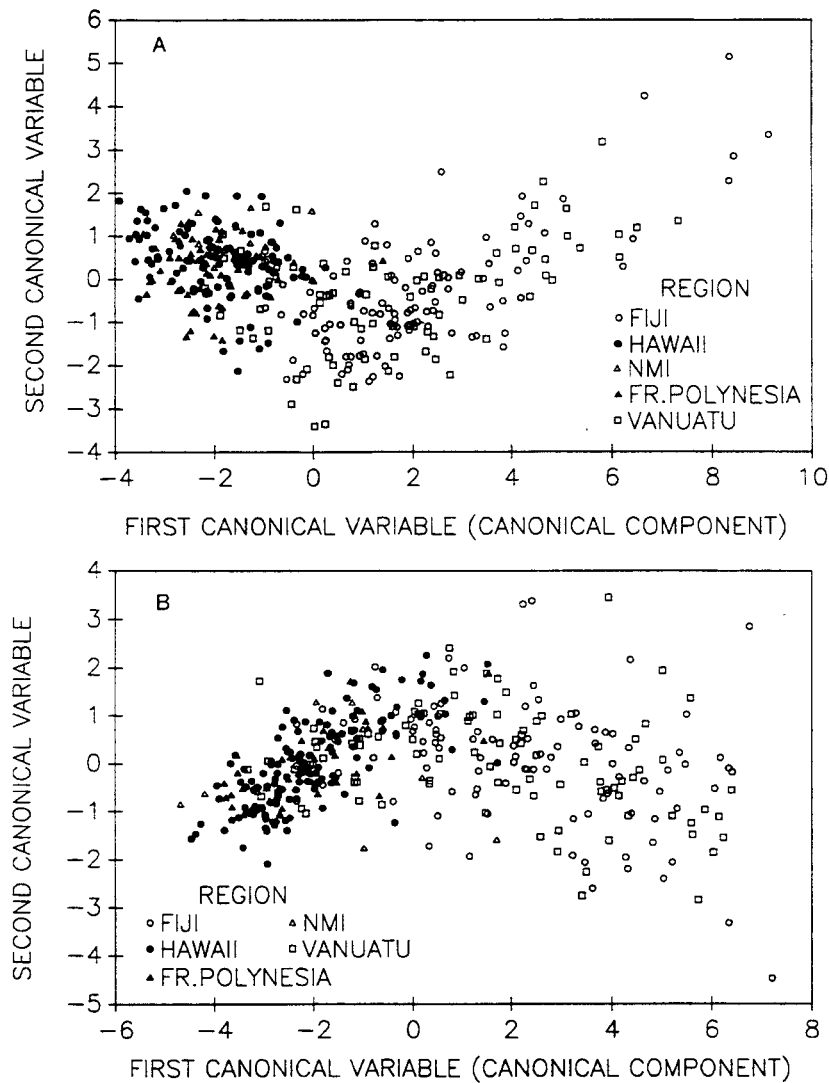


FIG. 2. Plot of canonical discriminant functions from (A) seven linear dimensions, circularity, and rectangularity and (B) 10 FFT harmonics (lateral view) for otoliths of the red snapper.

and localized declines in abundance of this species throughout the Pacific in response to fishing pressure (Schaan et al. 1987; Ralston and Kawamoto 1987; Carlot and Cillaurren⁶; Latu and Tulua (see footnote 2); Nath and Sesewa (see footnote 4)) are an indication of low rates of migration and relatively slow growth which, together with the distance and depth between suitable habitat, lend themselves to the development of regional variation.

Regional differences in growth rate may be a primary factor in the development of differences in otolith shape. The simi-

larity in shape of otoliths from such widely separated regions as NMI, French Polynesia, and the Hawaiian Islands suggests that growth rate represents an important component of otolith shape. These regions have slow or limited growth in common and had thicker, heavier, and more rounded otoliths. Available estimates (Uchida et al. 1982; Brouard et al. 1983; Brouard and Gradperrin 1985; Ralston and Kawamoto 1987; Ralston and Williams 1988; Carlot and Nguyen 1989) indicate that ehu from the southwestern Pacific grow considerably faster than those from Hawaii, NMI, and French Polynesia. Fish from NMI may initially grow at a similar rate to those from the southwestern region (Smith and Kostlan 1991), but do not reach comparably large sizes. Differences in otolith shape may be mediated through differences in the orientation and packing in

⁶A. H. Carlot and E. Cillaurren. Present status in yield assessment for deep bottom fishery in Vanuatu. Contrib. Fish. Dep. and ORSTOM, Port Vila, Vanuatu. USAID/NMFS Trop. Fish. Res. Assess. Workshop, July 1989, Honolulu, HI. 17 p. (Manuscr.)

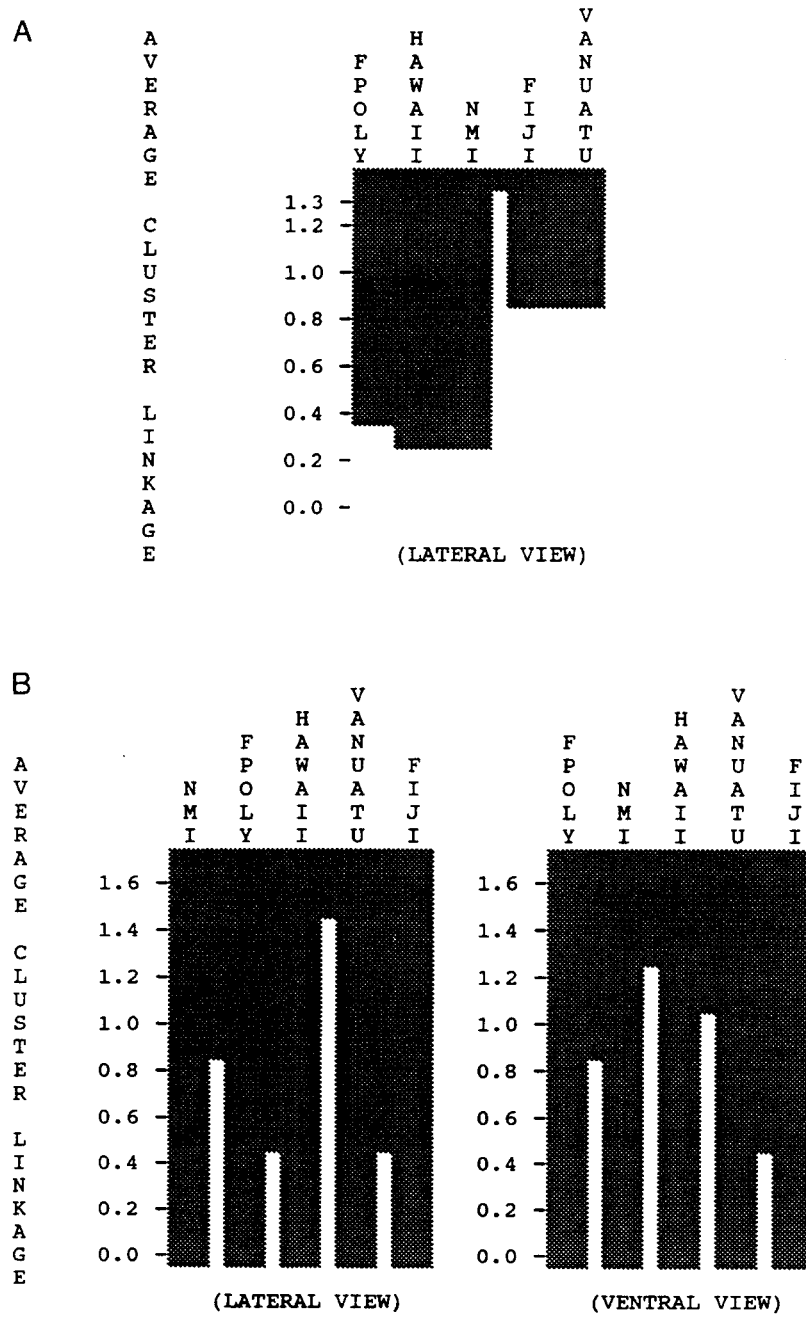


FIG. 3. Hierarchical clusters (cluster dendograms in the style of Johnson 1967) of regional otolith samples based on (A) six linear proportions, circularity, and rectangularity and (B) 20 harmonics.

the otolith crystal, which could easily be influenced by the rate of crystalline growth.

Growth-related differences in linear otolith proportions have been described for other species (Reznick et al. 1989; Secor and Dean 1989). Gaemers and Crapon de Craona (1986) referred to a sexual dimorphism in otoliths of haplochromines. Faster growing males of these cichlids have more elongate and thinner otoliths. Gaudie et al.⁷ described differences in otolith shape as a function of parasite load for orange roughy (*Hoplostethus atlanticus*). Slow-growing parasitized fish had thicker and wider otoliths. Wilson (1985), describing compensatory depth-related differences in otolith shape for macrourids from the Atlantic and Pacific oceans, found that otoliths were either long and thin or short, wide, and thick. The shape differences noted by Wilson may be attributable to regional and depth-related differences in temperature and/or fish growth rates.

Data compiled by the National Oceanographic Data Center (NODC) (1989) show that mean temperatures at 150–400 m, where ehu are found, are 2–6° lower for Hawaii and NMI than for Fiji and Vanuatu. Temperatures for French Polynesia were 2–3° lower between 275 and 400 m, but were comparable with Fiji and Vanuatu above that depth. Uncoupling of somatic and otolith growth rates as a function of temperature has been described in the literature (Mosegaard et al. 1988). Whether differences in temperature affect otolith shapes directly or through temperature-related constraints on somatic growth cannot be determined from this study. Other factors (such as differences in feeding and food availability between locations) may also be responsible for regional variation in size. Information on habitat, population biology, and morphology of *Etelis carbunculus* must eventually be tied together to evaluate the causes of regional size and shape differences in this species.

Ehu provide an illustration of the continuous changes in shape taking place in otoliths throughout the life cycle. Changes in otolith shape in larval fishes are well known, but post-juvenile shape differences are rarely mentioned in the literature. These changes may be related to shifts in the metabolic rate (Gaudie 1990) as fish mature.

This summary of otolith measurements in several dimensions makes it clear that the otolith does not grow at a constant rate along all axes. For this reason, several planes of sectioning must be considered before attempting to interpret growth from seasonal, annual, or daily growth marks obtained from sections of the otolith (Radtko 1987). Due to the changing relationship between fish age (or size) and otolith shape, regressions of fish length versus linear otolith measurements in any dimension will vary as a function of the size range and number of fish from which data are obtained. The complexity of considerations to be made in selecting a representative size range and number of samples for a given population is illustrated by the fact that the foregoing comparisons between fish of different sizes were affected by size-specific differences in otolith shape, despite the fact that shape indices were scaled to size. Thus, the importance of careful planning to collect a representative sample for the determination of growth parameters must be stressed.

Otolith morphology has long been used in stock differentiation (Einarsson 1951; Zijlstra 1958; Kotthaus 1961; Messieh 1972; Postuma 1974), but recently, otoliths have become

⁷R. W. Gaudie, J. B. Jones, and S. Bellara. Genotype and parasite load components of the variation in the shape of the otolith of the orange roughy. Fisheries Research Centre, Wellington, New Zealand. 22 p. + figures. (Manuscr.)

increasingly popular for their timekeeping properties. As Fourier series (Bird et al. 1986; Gaudie and Nelson 1990; Castonguay et al. 1991), scanning electron microscopy (Davies et al. 1988; Gaudie et al. 1990), and other methods make it increasingly feasible to discern differences in otolith shape and molecular structure, researchers have begun to point out a wide range of inter- and intrapopulation differences in otolith shape. Differences in the morphology of otoliths of *Etelis carbunculus* were first believed to be an indication of taxonomic differences in stocks. However, while regional stocks fit the species description, otolith morphology proved to be quite varied and complex. The three-dimensional variation in otolith growth rate described herein represents another indication that growth estimation from single-plane sectioning may someday be viewed as an oversimplification. Since a better understanding of the determinants of otolith structure is paramount to the interpretation of age and growth in fishes, as well as to discussions of stock differentiation and otolith taxonomy, these findings may eventually have more far-reaching applications.

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