Geographic Variation in Morphometric Characters and Gill-Raker Counts of Yellowfin Tuna *Thunnus albacares* from the Pacific Ocean

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Abstract.—Samples of yellowfin tuna *Thunnus albacares* from five different areas of the Pacific Ocean, Mexico, Ecuador, Australia, Japan, and Hawaii, collected during January to May of 1988, were examined for geographic variation in morphometric characters and gill-raker counts. The Kruskal-Wallis test indicated a significant difference in the total gill-raker counts among areas. The morphometric data were adjusted by allometric formulae to remove size effects. The overall percent-correct classification rate for the five groups from the stepwise discriminant analysis, based on 12 adjusted morphometric characters, was 77.6%. This is 72.0% (Cohen's kappa statistic) better than would have occurred by chance. These results indicate significant meristic and morphological differences of yellowfin tuna from these areas, which suggests that fish from these areas represent separate groups.

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Yellowfin tuna *Thunnus albacares* is an epipelagic species found worldwide in tropical and subtropical oceanic regions, with a nearly continuous distribution in the Pacific Ocean from roughly 40°N to 40°S (Collette and Nauen 1983). The large-scale industrial fisheries for tuna in the Pacific Ocean landed an estimated 471 thousand metric tons of yellowfin tuna in 1985 (Joseph 1987). Fundamental to the proper management of yellowfin tuna is the elucidation of population structure. The interactions among existing, expanding, or developing fisheries on this resource cannot be assessed without this knowledge.

Morphometric studies have provided results useful for identifying marine fish stocks and describing their spatial distributions (Ihssen et al. 1981, Winans 1987). Morphometric characters, used extensively in the analysis of population structure of yellowfin tuna, indicate that there are at least three groups in the Pacific Ocean. Godsil (1948) and Godsil and Greenhood (1951) identified four stocks of yellowfin tuna in the Pacific (Japan, Hawaii, Peru, and the northeastern Pacific) from morphometric characters. Morphometric data indicate that yellowfin tuna from southeastern Polynesia, Hawaii, and Central America are different stocks (Schaefer 1955). Kurogane and Hiyama (1957) concluded from morphometric data that there are three stocks in the Pacific: western, central, and eastern. Royce (1964), however, concluded that there is an apparent cline in morphometric characters along the equator from off Costa Rica to the Caroline Islands. Suzuki et al. (1978) reviewed fisheries and biological data, including morphometric data, and concluded that there are at least three relatively independent stocks: western, central, and eastern Pacific. More recently, Schaefer (1989) showed morphometric differences between yellowfin tuna from north and south of 15°N–20°N in the eastern Pacific Ocean. With the exception of Schaefer's (1989) study, previous investigations primarily utilized univariate analyses of morphometric characters. Although geographic variation in yellowfin tuna morphology can be demonstrated in this manner, univariate analyses of single characters do not permit the classification of individual fish into discrete groups or stocks.

The objectives of the present study were to (1) assess and describe geographic variation in morphological characters and gill-raker counts of yellowfin tuna from five widely-scattered locations of the Pacific basin, (2) test the hypothesis of morphometrically distinguishable northern and southern groups in the eastern Pacific, and (3) identify the

best set of characters for group separation. I examined gill-raker counts because this meristic character appeared useful in separating groups of Pacific yellowfin tuna (Godsil and Byers 1944, Schaefer 1955). Rather than using the term "stock(s)," since it is not known whether there is a genetic component to the differences observed, I use the term "group(s)," as defined by Marr (1957), because this avoids the technicality of the degree to which genetics are involved in the differences observed.

Materials and methods

Sampling and data collection

Yellowfin tuna were captured by baitboats, trollers, or sportfishing boats during January to May 1988, from five localities in the Pacific Ocean: the Revillagigedo Islands, Mexico; Manta, Ecuador; New South Wales, Australia; Ishigaki, Japan; and Oahu, Hawaii (Fig. 1). These locations were selected to optimize spatial coverage within the distribution of the surface and longline fisheries for yellowfin tuna in the Pacific. Samples ranged from 66 to 105 individuals per location (Table 1), and included fish from at least four schools from each area.

Thirteen linear measurements (Fig. 2) were made with calipers on each specimen within 24 hours of capture, and recorded to the nearest millimeter, according to methods described by Marr and Schaefer (1949). The number of gill rakers on the upper and lower limbs of the first left gill arch were also recorded for each fish. Counts for the lower limb included the single gill raker present at the angle between the upper and lower limbs (Collette and Nauen 1983). Sex was determined by examination of the gonads of the fish from Ecuador and Australia, and this subset of fish was used to test the hypothesis of no sexual dimorphism in morphometric characters of yellowfin tuna.

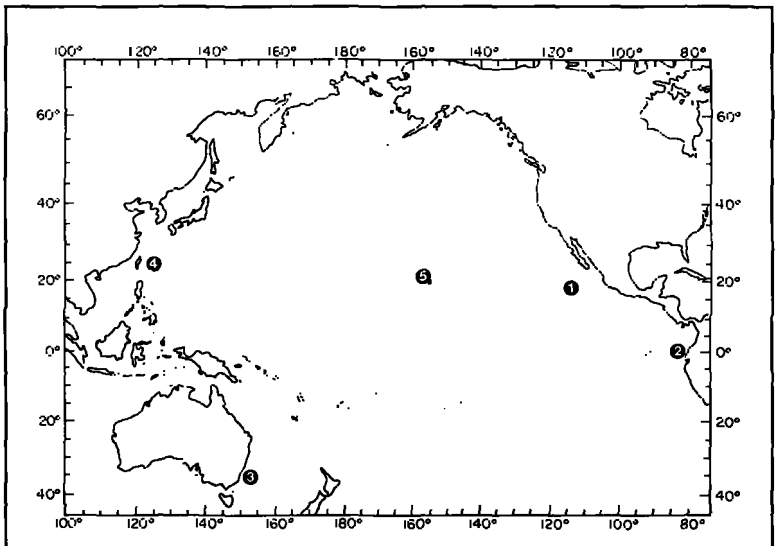


Figure 1
Sampling locations in the Pacific Ocean for yellowfin tuna: (1) Revillagigedo Islands, Mexico; (2) Manta, Ecuador; (3) New South Wales, Australia; (4) Ishigaki, Japan; and (5) Oahu, Hawaii.

Table 1
Summary statistics for total length in millimeters, by area, for 452 yellowfin tuna.

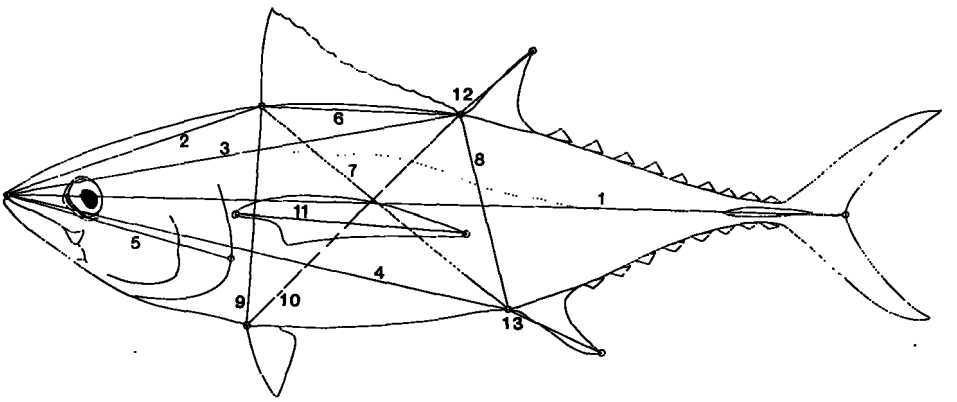
Sample	n	Mean	SD	Min.	Max.
Mexico	101	635.4	151.7	444	983
Ecuador	80	532.9	101.4	431	789
Australia	66	853.9	49.4	690	990
Japan	100	567.9	142.3	434	956
Hawaii	105	604.7	87.8	452	826

Statistical analyses

Because of the variation in size of fish from different areas (Table 1), morphometric data were statistically adjusted to permit comparative analysis in terms of shape independently of size (Gould 1966, Thorpe 1983).

The morphometric measurements were first transformed to common logarithms because linearity and multivariate normality are usually more closely approximated by logarithms than by the original variables (Pimentel 1979). Outliers were detected by regression analyses of morphometric characters against total length and by scatter plots of residuals versus predicted values (Cook and Weisburg 1982). When an outlier was found, all the morphometric data (but not the gill-raker data) for that fish were withdrawn from further consideration. This procedure resulted in the elimination of morphometric data for 23 fish.

Each of the morphometric characters showed a linear relationship with total length (r^2 ranged from 0.95 to 0.99), when analyzed by geographic region. Analysis of covariance (ANCOVA) was employed to test for differences in allometric relationships among samples, and to estimate the common within-group regression slopes. Within-group regression slopes were significantly different ($P<0.01$) for 10 of the morphometric characters, and thus size adjustments were based on the common within-group slopes. Coefficients from the



Acronym	Morphometric Character
TL	Total length
SFD	Snout to insertion of first dorsal fin
SSD	Snout to insertion of second dorsal fin
SAF	Snout to insertion of anal fin
HL	Head length
FDSD	Insertion of first dorsal fin to insertion of second dorsal fin
FDAF	Insertion of first dorsal fin to insertion of anal fin
SDAF	Insertion of second dorsal fin to insertion of anal fin
FDPF	Insertion of first dorsal fin to insertion of pelvic fin
SDPF	Insertion of second dorsal fin to insertion of pelvic fin
PFL	Pectoral fin length
SDFL	Second dorsal fin length
AFL	Anal fin length

Figure 2

Morphometric characters measured and acronyms used for analysis of geographic variation of Pacific yellowfin tuna.

common within-group regression are used to allometrically adjust variates when between-group heterogeneity exists (Thorpe 1976, Reist 1985 and 1986). The measurements of the morphometric characters were adjusted to those expected for the overall mean total length with a modification of the allometric formula given by Thorpe (1975):

$$\hat{Y}_i = \log_{10} Y_i - [\beta(\log_{10} X_i - \log_{10} \bar{X})]$$

where

$\hat{Y}_i$ = adjusted logarithmic character measurement of the ith specimen,

Y_i = unadjusted character measurement of the ith specimen,

β = common within-group regression coefficient of $\log_{10} Y$ against $\log_{10} X$,

X_i = total length of the ith specimen, and

$\bar{X}$ = overall mean total length.

Reist (1985) has shown that this allometric adjustment effectively removes size variation from the data he examined. This statistical approach used to remove size effects from morphometric data has been shown to be an appropriate procedure for objective analysis of the data when there is size overlap among the groups examined (Claytor and MacCrimmon 1986).

I did not adjust gill-raker counts because Spearman's rank correlation procedure indicated that there were no significant correlations between gill-raker counts and total lengths. The Kruskal-Wallis test and a nonparametric multiple comparison test (Zar 1974) were utilized to test for differences among gill-raker counts from the five areas.

I used canonical variate analysis to examine the size-adjusted morphometric data for yellowfin tuna from five locations in the Pacific Ocean. This technique, also known as multiple discriminant function analysis (Pielou 1977), is appropriate when separation of more than

two groups is desired. Canonical variates are the scores from the individual discriminant functions; that is, they are linear combinations of the original variables. The graphical display of canonical variates (for example, canonical variates 1 and 2) is useful for demonstrating differences among groups because fish that belong to the same group appear closer together on the plot than fish from different groups. Ninety-five percent confidence circles (Pimentel 1979) for group centroids can also be calculated and plotted. In addition, canonical variates can be used to examine the effectiveness of the size-adjustment procedure. Thus, canonical variates 1 and 2 were regressed against total length, and size was considered to be effectively removed if regressions were not significant (Claytor and MacCrimmon 1986).

Stepwise discriminant analysis was used to choose the combination of variables that "best" separates the groups. The resultant discriminant function was then used to classify individual fish into groups. The discriminant analysis was applied to the adjusted morphometric characters with variables entered in a forward manner using $F = 4.0$ for entering, and $F = 3.996$ for removal. The expected actual error rates of the classification function were estimated using Lachenbruch's holdout procedure (Lachenbruch and Mickey 1968, Lachenbruch 1975, Johnson and Wichern 1982). This procedure provides less biased estimates of the misclassification rate than the resubstitution method (Lachenbruch 1975). The holdout procedure, or leaving-one-out method, is based on the classification of single observations that were withheld from model development and later classified. Cohen's kappa (κ) statistic and associated 95% confidence intervals were used to determine the improvement over chance of the percent-correct classification rates (Titus et al. 1984). Given five groups, the chance of correctly classifying a single fish is 20%.

All statistical analyses were performed on a MicroVax 3500 computer. MINITAB (Ryan et al. 1976) was used to perform regression analyses and ANOVA procedures; BMDP (Dixon et al. 1981) was used to perform ANCOVA procedures and discriminant function analyses.

Results

Data from male and female yellowfin tuna were pooled in subsequent analyses because two-sample t tests for mean values of adjusted morphometric characters and gill-raker counts of fish from Ecuador and Australia indicated no significant differences between sexes (Table 2).

Total gill-raker counts and counts from the upper limb and lower limb were significantly different ($P < 0.01$) among yellowfin tuna from the five areas (Table 3). Results from the multiple comparison test for the total gill-raker-count data indicate no significant difference between the rank sums for Australia and Japan and those for Mexico and Hawaii, but these pairs are significantly different from each other and from those of Ecuador. Total gill-raker counts appeared to be a better discriminator than either the upper or lower limb counts.

The regressions for canonical variables 1 and 2 against total length (r 0.17, $P = 0.14$, and r 0.22, $P = 0.09$) were not significant, indicating that size effects had been removed from the morphometric variates. The plot of the first two canonical variates, which account for 57% and 26% of the total variation, shows complete separation of the centroid values for each

Table 2

Summary of two-sample t test for differences among male and female yellowfin tuna for 12 morphometric characters adjusted for total length, and gill-raker counts, by areas. Definitions of character acronyms are given in Figure 2. None of the t statistics are significant at $P = 0.05$.

	Ecuador			Australia		
		Mean			Mean	
Character	t	Male n 45	Female n 33	t	Male n 37	Female n 27
SFD	0.31	2.29	2.29	−1.29	2.28	2.28
SSD	0.87	2.53	2.53	0.39	2.53	2.53
SAF	0.57	2.57	2.57	0.13	2.57	2.57
HL	−1.01	2.24	2.24	−0.66	2.23	2.23
FDSD	−0.42	2.18	2.18	1.12	2.19	2.19
FDAF	0.35	2.37	2.37	0.78	2.38	2.38
SDAF	−1.04	2.18	2.19	−0.14	2.18	2.18
FDPF	−1.00	2.34	2.34	0.64	2.35	2.35
SDPF	−1.12	2.17	2.17	1.16	2.19	2.19
PFL	0.85	2.21	2.21	−0.95	2.24	2.25
SDFL	0.94	1.85	1.84	−1.52	1.91	1.92
AFL	1.07	1.83	1.83	−0.92	1.90	1.90
Gill rakers						
Upper limb	1.06	9.36	9.24	0.60	8.28	8.19
Lower limb	−0.04	21.45	21.46	−0.30	20.98	21.04
Total	−0.64	30.74	30.87	−0.81	29.27	29.48

Table 3

Gill-raker counts (means ± SD) and associated H values (Kruskal-Wallis, df 4) for yellowfin tuna from five locations in the Pacific Ocean. $^*P<0.01$.

Character	Mexico (n 101)	Ecuador (n 80)	Australia (n 66)	Japan (n 100)	Hawaii (n 100)	All (n 447)	H
Upper limb	8.4 ± 0.6	9.3 ± 0.5	8.2 ± 0.5	8.3 ± 0.6	8.4 ± 0.6	8.5 ± 0.7	127.18*
Lower limb	21.6 ± 0.8	21.5 ± 0.8	21.0 ± 0.8	21.2 ± 0.8	21.9 ± 0.7	21.5 ± 0.9	52.20*
Total	30.0 ± 1.1	30.8 ± 0.9	29.2 ± 1.0	29.5 ± 1.1	30.2 ± 1.0	30.0 ± 1.1	92.56*

group, as indicated by the 95% confidence circles for population centroids (Fig. 3). Although there is noticeable overlap of individuals, particularly of fish from Mexico and Ecuador, the fish of the eastern Pacific (Mexico and Ecuador) are fairly distinct from those of the central (Hawaii) and western Pacific (Australia and Japan). The samples from Japan and Hawaii appear to be more similar than those from Australia and Japan. The canonical variate analyses suggest that size-adjusted morphometric characters are useful for the delineation of yellowfin tuna groups. I then used stepwise discriminant function analysis to identify the most useful characters and to estimate the classification function. The stepwise analysis revealed that 11 of the 12 adjusted morphometric characters contributed significantly to the multivariate discrimination of the five groups of fish (Table 4). The approximate F statistic computed from Mahalanobis D^2 indicates a significant difference among the five groups ($F_{0.05}$ = 40.77, df 44,1585.8, $P<0.01$). The correct classification rates estimated from the holdout procedure for the 11-variable discriminant function ranged from 61.5 to 95.3%, with an overall rate of 77.6%, which is 72.0% (κ) better than would have occurred by chance (95% confidence intervals: $67.0\% \leq \kappa \leq 77.0\%$).

Pectoral fin length (PFL) is the single most useful character for distinguishing yellowfin tuna from the five groups (Fig. 4). Yellowfin tuna from Mexico and Ecuador can be distinguished from one another and from those from Australia, Japan, and Hawaii by this character alone (Newman-Keuls multiple range test). In addition to shorter PFL of fish from the eastern Pacific, the second dorsal fin length and anal fin length are shorter, relative to those of fish from Australia, Japan, and Hawaii. Head length, however, is shorter for fish from the western Pacific.

Because I was interested in improving the ability to delineate fish from Mexico and Ecuador, morphometric characters of these fish were readjusted and subjected to a second stepwise discriminant analysis. The common within-group slopes were used to adjust the morphometric characters to those expected for the overall mean total length for these two groups, employing the

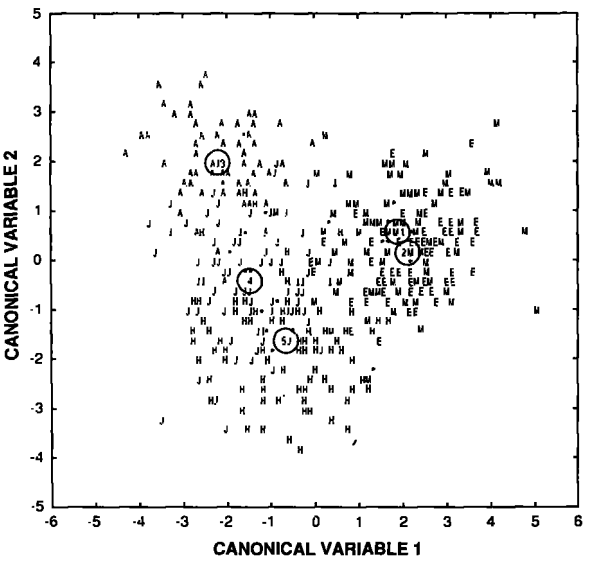


Figure 3

Plot of individuals, group centroids, and 95% confidence circles for population centroids on canonical variables 1 and 2 for the five groups of yellowfin tuna, based on 12 adjusted morphometric characters. Symbols for individual fish: M = Mexico, E = Ecuador, A = Australia, J = Japan, H = Hawaii. Overlap of individuals from different groups is indicated by asterisks. Symbols for group centroids: 1 = Mexico, 2 = Ecuador, 3 = Australia, 4 = Japan, 5 = Hawaii.

previous formula. The regression of the discriminant function score against total length was not significant (P = 0.37), indicating that size effects had been removed by the adjustment procedure. The frequency distribution of the canonical variable (Fig. 5) shows fairly good separation into the two groups, with only a small amount of overlap. Results of the stepwise discriminant analysis are presented in Table 5. The correct classification rate for the fish from Mexico and Ecuador was 81.3% and 88.5%, respectively, with an overall rate of 84.6%, which is 69.3% (κ) better than would have occurred by chance (95% confidence interval: $58.3\% \leq \kappa \leq 80.3\%$). Fish from the two groups were significantly different ($F_{0.05}$ = 40.00, df 6,162, $P<0.01$).

Table 4

Summary of stepwise discriminant analysis for 5 groups and 12 adjusted morphometric characters of yellowfin tuna. Character acronyms are defined in Figure 2.

Step number	Variable entered	F value to enter or remove	Number of variables included	Approximate F-statistic	Degrees of freedom	
1	PFL	154.39	1	154.39	4	424
2	SDFL	78.92	2	113.28	8	846
3	FDPF	47.73	3	92.76	12	1116.80
4	SFD	38.58	4	81.71	16	1286.81
5	HL	21.04	5	70.77	20	1393.93
6	SDPF	15.86	6	62.62	24	1462.93
7	SDAF	14.03	7	56.67	28	1508.54
8	AFL	10.24	8	51.53	32	1539.42
9	FDSD	8.09	9	47.20	36	1560.68
10	FDAF	8.01	10	43.79	40	1575.49
11	SSD	6.44	11	40.77	44	1585.82

Classification results

Group	n	Percent correct	Number of fish classified into group				
			Mexico	Ecuador	Australia	Japan	Hawaii
Mexico	91	75.8	69	14	2	3	3
Ecuador	78	84.6	5	66	1	4	2
Australia	64	95.3	0	0	61	3	0
Japan	96	61.5	3	0	13	59	21
Hawaii	100	78.0	3	3	4	12	78
Total	429	77.6					

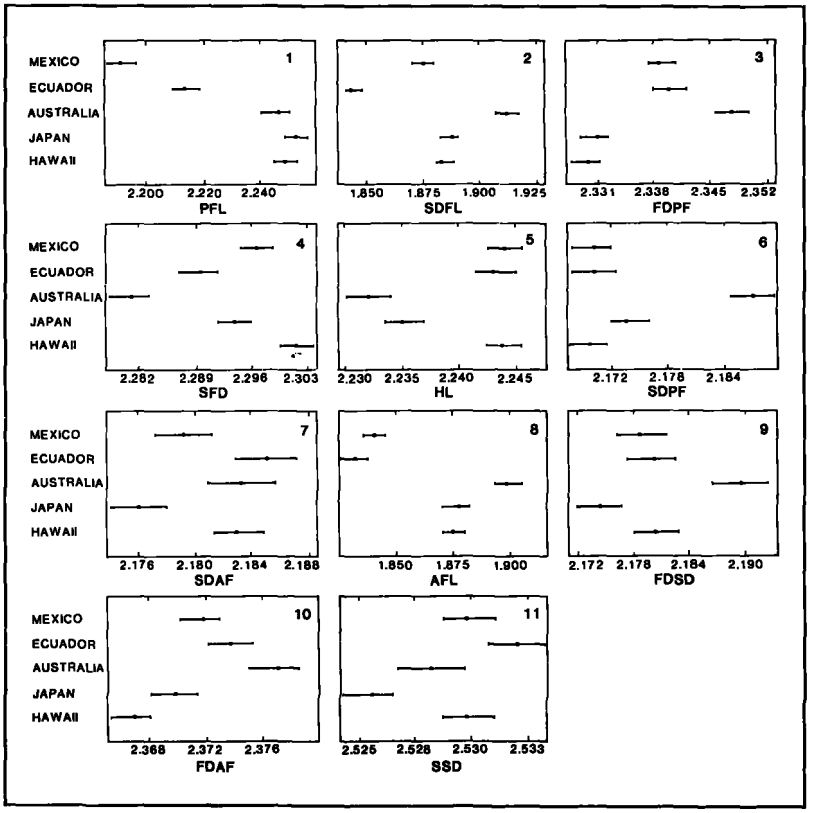


Figure 4

Means and individual 95% confidence intervals based on pooled standard deviations for morphometric characters adjusted for total length, for five yellowfin tuna sample areas in the Pacific Ocean, and the order in which they entered the stepwise discriminant analysis. Character acronyms are defined in Figure 2.

Discussion

The results of these analyses of morphometric characters and gill-raker counts suggest that each of the areas included in this investigation is inhabited by a discrete group of yellowfin tuna.

Yellowfin tuna from the eastern Pacific are morphologically more similar to one another than are fish from the central and western Pacific, as shown by the amount of overlap in the samples from Mexico and Ecuador relative to those of Australia, Japan, and Hawaii (Fig. 3). The overlap of samples from the eastern Pacific may be due to a greater degree

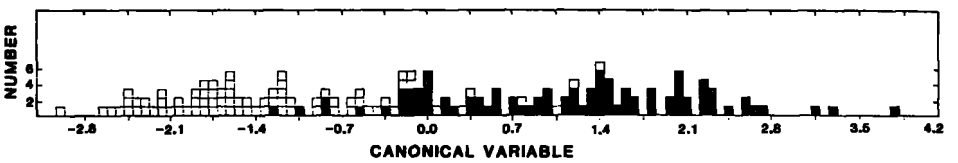


Figure 5

Frequency distribution of individual canonical scores based on 12 adjusted morphometric characters for yellowfin tuna from Mexico (open squares) and Ecuador (black squares). Centroid values for Ecuador and Mexico are −1.31 and 1.12, respectively.

Table 5

Summary of stepwise discriminant function analyses for Mexico and Ecuador groups and 12 adjusted morphometric characters of yellowfin tuna. Character acronyms are defined in Table 2.

Step number	Variable entered	*F* value to enter or remove	Number of variables	Approximate *F*-statistic	Degrees of freedom
1	SDFL	120.116	1	120.116	1 167
2	PFL	25.336	2	81.478	2 166
3	SFD	12.282	3	62.104	3 165
4	SDAF	12.988	4	53.209	4 164
5	SSD	4.730	5	44.481	5 163
6	FDSD	8.022	6	40.002	6 162

Classification results

			Number of fish classified into group	
Group	*n*	Percent correct	Mexico	Ecuador
Mexico	91	81.3	74	17
Ecuador	78	88.5	9	69
Total	169	84.6		

of mixing of the groups of fish within this region. My results agree with other studies on the morphometrics of yellowfin tuna from the Pacific Ocean: morphological differences exist among fish in the eastern, central, and western Pacific (Godsil 1948, Godsil and Greenhood 1951, Schaefer 1955, Kurogane and Hiyama 1957, Royce 1964).

One of the objectives of this study was to further evaluate the previously reported morphometric differences between northern and southern groups in the eastern Pacific (Schaefer 1989). The morphometric analysis of yellowfin tuna from the eastern Pacific by Schaefer (1989) was based upon samples from 55 locations and comprised a total of 2701 fish collected during 1974–76. Only the first eight morphometric characters shown in Figure 2 of this study were recorded and included in the analyses of that investigation. The correct classification rates from the discriminant analysis of the morphometric data from yellowfin tuna sampled from north of 15°N–20°N was 68.0%, and for those sampled from the south was 73.7%; the overall correct classification rate was 72.1%. In this study two additional morphometric characters (second dorsal and pectoral fin lengths) were selected first and second in the stepwise discriminant analysis of morphometric characters of fish from Mexico and Ecuador, indicating their discriminatory power (Table 5). The correct classification rate from the discriminant analysis for these two groups was 84.6% (Table 5). The correct classification rate from the discriminant analysis for these two groups, using the eight morphometric characters (Fig. 2) investigated by Schaefer (1989), was only 68.6%.

Total gill-raker counts of yellowfin tuna appear to be important characters which permit separation of fish from the eastern, central, and western Pacific. This meristic character also has the potential for separation of fish on a latitudinal scale as clearly indicated by the

separation of fish from Mexico and Ecuador. The gill-raker counts reported by Godsil and Byers (1944) are based upon relatively few fish from several widely scattered locations in the Pacific, but show differences between fish from Japan and those from Hawaii, Ecuador, and northern Mexico. Differences in the gill-raker counts of fish from Central America and from Hawaii have been reported by Schaefer (1955).

I recommend the use of gill-raker counts for separation on a broad geographic scale. However, this character alone is not adequate for the discrimination and classification of individuals from selected geographical locations, and should thus be collected in conjunction with morphometric data to allow finer resolution within major oceanic areas. Because 11 of the 12 adjusted morphometric characters contributed significantly to the stepwise discriminant analysis (Table 4), and because none of the 13 characters (Fig. 2) are potentially difficult to measure, I consider the set of 13 characters utilized in this study to be appropriate for future investigations of tuna morphometrics.

Extensive tagging studies designed to investigate movements of yellowfin tuna have been conducted only in the eastern Pacific (Joseph et al. 1964, Bayliff 1979, Hunter et al. 1986). Movements of yellowfin tuna in the eastern Pacific tend to be restricted, with few individuals moving more than several hundred miles. Tagging of yellowfin tuna during 1968–74 in the eastern Pacific, in inshore and offshore areas, indicated few long-distance east-west or north-south movements of the fish. The results of the present study and that of Schaefer (1989) on morphometrics of yellowfin tuna in the eastern Pacific also suggest that movements are restricted. The results of this investigation appear to be in reasonably good agreement with those of tagging studies, although several tagged yellowfin tuna released in the central Pacific have been recaptured in the eastern Pacific, and a tagged yellowfin tuna released in the western Pacific was recaptured in the eastern Pacific after traveling a net distance of 3806 miles (Peterson 1983).

Observed morphometric and meristic differences in this investigation are probably influenced both by genes and environment. It would be valuable to conduct a study of the population structure of yellowfin tuna throughout the Pacific; morphometric and meristic data should be collected, along with tissue samples to be analyzed for genetic information. Both mitochondrial DNA and nuclear genes should be screened and analyzed (Avise 1987). This approach would address the genetic basis of the groups inferred from morphometric and meristic differences. The accumulated information from morphometrics, meristics, and genetics, along with other life-history information, could then be evaluated for a better understanding of the population structure of yellowfin tuna in the Pacific Ocean.

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