

USING OBJECTIVE CRITERIA AND MULTIPLE REGRESSION MODELS FOR AGE DETERMINATION IN FISHES

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ABSTRACT

Analysis of the age structure of exploited fish populations is necessary for models upon which management decisions are made, but existing aging methodology for many species is hindered by subjective criteria used in age determination. A new technique is described in which age is estimated using multiple regression models based upon the measurable parameters otolith weight, otolith length, and otolith width in the splitnose rockfish, *Sebastes diploproa*, and the canary rockfish, *S. pinniger*. Models were calibrated using ages determined by interpretation of both whole otoliths and otolith sections which differ within these species, particularly at greater lengths. The models typically explained from 70 to 92% of the variability in age depending upon species, sex, and method of age analysis. In another sample used to verify the precision of the models, variability associated with model-estimated ages was generally less than that induced by variability in ages between different agencies. Based upon the pattern of otolith growth in length, width, and weight in these and other species, it is suggested that these methods would be applicable to a wide variety of fishes. Implementation of this type of age determination methodology could result in savings in time and cost for fisheries management agencies while decreasing variability among age estimates between different laboratories.

Virtually all methods of age determination in fishes involve a certain degree of subjectivity. Deciding whether a mark on an otolith or scale constitutes 1 year's growth is difficult; precision in fish aging improves only with experience. Even so, variability between experienced readers may be great. Sandeman (1969), for example, observed only 9% agreement between readers for a wide age range of otoliths of *Sebastes marinus* and *S. mentella*, and noted greater variability with increasing age of the fish. Kimura et al. (1979) suggested that bias between readers within a given agency is likely to be much less than among different agencies. In a situation such as exists on the Pacific coast, where several management agencies may routinely determine ages for the same species, interagency calibrations are necessary but are rarely achieved. Williams and Bedford (1974) suggested "... that otolith reading remains, for the present at least, as much an art as a science, and that proficiency cannot easily be achieved without examination of very large numbers of otoliths." Clearly, objective, repeatable age determination methodology which will minimize variability is desirable.

Traditional methodology for age determination

in fishes generally involves some calcified structure; in *Sebastes*, Six and Horton (1977) tested 25 different structures. By far the most commonly used structures, however, are the otolith and scales. Scales are often best for short-lived, fast-growing species because annuli become indistinct near the margin in long-lived, slower growing species (Power 1978; Maraldo and MacCrimmon 1979). When this is the case, the otolith becomes the superior structure for age determination; even in the otolith, however, annuli may become indistinct on the margin as otoliths thicken and become opaque with age. For this reason several investigators have used broken or sectioned otoliths to determine age from internal banding patterns. While some studies using otolith sections have provided clear continuation of growth patterns obvious on whole otoliths from younger specimens, others have suggested maximum ages which are double or triple those estimated from whole otoliths. Power (1978), for example, suggested ages of >50 yr in *Salvelinus namaycush* and *Coregonus clupeaformis* and provided confirming evidence based upon population structure. In the redbfish, *Sebastes marinus*, Sandeman (1961) suggested that specimens exceeding 50 yr of age were present in the population; ages up to 80 yr have since been estimated (Sandeman²). Similarly, Beamish

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MATERIALS AND METHODS

Otolith Collection

Otoliths of *S. pinniger* and *S. diploproa* were collected during the 1980 West Coast Survey conducted by the Northwest and Alaska Fisheries Center on the FV *Pat San Marie* and the FV *Mary Lou*. Gear and sampling strategy were similar to that described in Gunderson and Sample (1980). Otoliths were collected from fish captured in all hauls until desired numbers of specimens in specified length categories were obtained. Both otoliths from each specimen were removed, cleaned, and stored in individual, labeled vials containing 50% ethanol. Data taken with each specimen included vessel, haul (with latitude, longitude, and bottom depth), sex, and fork length (to the nearest 0.1 cm). After returning to the laboratory, otoliths were thoroughly cleaned and the preservative renewed.

Age Determination

General information on otolith morphology and whole otolith aging methodology in *Sebastes* is described in detail by Kimura et al. (1979). Age determined from whole otoliths followed the aging methodology of Boehlert (1980) for *S. diploproa* and that of Six and Horton (1977) for *S. pinniger*. Ages determined in this manner are referred to as whole otolith ages.

Otolith sections were prepared for selected specimens using the left otolith after the methodology of Nichy³ with several modifications. Specimens were affixed to heavy-duty cardboard tags with double-faced tape and embedded in polyester casting resin in preparation for sectioning. Specimens were mounted in a chuck specifically designed to accommodate the cardboard tags and fed onto a pair of thin diamond blades separated by acetate spacers on a Buehler⁴ low-speed Isomet saw. Dorsal-ventral sections through the focus and perpendicular to the sulcus, about 0.4 mm thick, were removed from the center of the otolith. Sections were removed from the tag and attached to labeled microscope slides with histological mounting medium. They were subsequently ground to eliminate surface artifacts,

(1979b) estimated ages approaching 90 yr in certain Pacific species of *Sebastes*, including *S. alutus*. In the genus *Sebastes*, these estimates of extended longevity have recently been confirmed by Bennett et al. (1982), who used geochronological methods to confirm age in *S. diploproa*. Understanding population structure for such long-lived species will require a large number of age estimates using otolith sections. Routine sectioning and interpretation of otoliths, however, is a time-consuming process, and age structure would need to be determined frequently for management of an active fishery. In this paper I suggest a possible alternative method for age determination.

Otolith growth begins with the initial "focus" and thereafter by incremental concretions of calcium carbonate in the form of aragonite. Otolith size increases with increasing size and age of the fish. Differential addition of crystalline material to the otolith, however, results in a species-specific shape (Bingel 1981). In flatfish and certain other species, Williams and Bedford (1974) observed continued linear growth of the otolith with growth of the fish only until maximum size was achieved; beyond this time, the otolith began to thicken. This has been observed in several other species (Blacker 1974a). Linear measurements of the otolith (i.e., length and width) are directly related to fish length and show little variability, but otolith thickness and weight are highly variable in larger fish (Templeman and Squire 1956; Beamish 1979a, b).

Templeman and Squire (1956) observed that length and width of otoliths from slow- and fast-growing populations of haddock did not differ at the same fish length, whereas otolith weight was consistently greater in the slower growing (and therefore older) populations at a given length. The same trend appears to exist in some members of the genus *Sebastes* (G. W. Boehlert unpubl. data).

Beamish (1979a) observed an increase in thickness of the hake otolith with increasing otolith section age and a nearly linear relationship of otolith thickness and otolith weight. If otolith thickness, and therefore weight, is a function of fish age, then if fish length (or otolith length, since the two are related) is known, one should be able to estimate fish age. This was suggested by Brander (1974) with Irish Sea cod. The objective of this study is to determine the trends of otolith growth in terms of thickness, length, width, and weight, and to determine the potential of these criteria for estimation of age in splitnose rockfish, *S. diploproa*, and canary rockfish, *S. pinniger*.

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⁴Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

first with 400-grit carborundum paper and then polished with 3 μm jeweler's rouge.

To compare internal otolith section annuli with surface annuli, 25 whole left otoliths from *S. pinniger* and 50 from *S. diploproa* were selected. Sample size was chosen to represent the range of ages estimated from whole otoliths. I determined the distance from focus to each annulus on the whole otolith along the dorsal-ventral axis from focus to dorsal edge of the otolith using an ocular micrometer on a dissecting microscope. These measurements were used to identify the first several annuli on corresponding sections. By following these identified annuli around to the internal dorsal surface it was determined that each small ring in the direction of counting (from focus to dorsal, interior surface) corresponded to a single year of growth (Fig. 1).

Sections were initially examined under a dissecting microscope at 30 \times magnification with either reflected light and a black background or transmitted light, depending upon the clarity of the annuli. Discerning and counting the narrow zones in otoliths from older fish was facilitated by the use of a compound microscope interfaced with a video camera and television screen. A more accurate estimate of age was made possible by the increased magnification and enhanced contrast of the compound microscope, coupled with the ease of viewing annuli on an enlarged screen.

Sections were aged by identifying the first translucent annulus (winter growth zone) and counting sequential growth zones from the center

to the dorsal edge. Subsequent annuli were followed from the dorsal edge to the interior dorsal quadrant (after Beamish 1979b), and counted to the internal surface. In this paper, ages determined by different methods and sources will be discussed; none of these ages is known with certainty. For this reason, given ages will be defined as "standard ages" only for purposes of comparison.

Calibration Subsample

To establish models of age based upon otolith dimension and weight criteria, otoliths from the entire collection were subsampled. Every fourth otolith pair of *S. diploproa* and every third of *S. pinniger* were selected to provide roughly equal sample sizes representative of all sizes and collection (latitudinal) areas. These subsampled otoliths were used to develop the multiple regression models (see section on Data Analysis) and were treated as described below.

Whole otolith ages were determined by an experienced otolith reader to whom fish length remained unknown. This practice has been recommended by Williams and Bedford (1974), among others, to minimize bias in otolith reading. Otoliths were then dried to a constant weight at 58°C and placed in a desiccator for 8 h. Intact left otoliths were weighed to the nearest milligram. Otoliths were measured with dial calipers in the anteroposterior dimension (length) to the nearest 0.02 mm and in the maximum dorsoventral di-

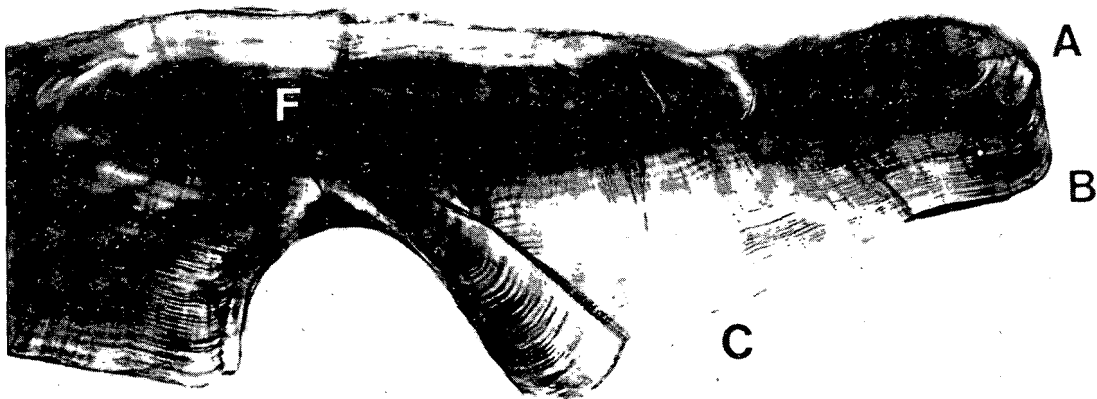


FIGURE 1.—Dorsal-ventral section of the left otolith of a 305 mm FL female *Sebastes diploproa*. Whole otolith ages are generally determined from the focus (F) to the dorsal edge (A), but often extend to the posterior margin (not shown) which may include additional annuli extending to greater ages (A to B). Section ages are determined from the focus (F) to the internal dorsal surface (C). Note the additional growth zones on axis F-C which have been deposited after the latest visible zones on axis F-A. The otolith section age of this specimen is 40 yr.

mension (width) to the nearest 0.05 mm. When the left otolith was chipped or broken, the right one was substituted for measurements, since no systematic differences between left and right otolith measurements were apparent for either species. The left otolith was subsequently sectioned and age determined by the same otolith reader. Otolith thickness, which is too variable to measure on the whole otolith, was measured on the section from internal to external surface just dorsal to the sulcus (Fig. 1).

Confirmation Subsample

In order to test the precision of the model, subsamples of 50 otoliths by sex and species were drawn randomly from samples not used in the calibration subsample. These samples were handled in the following way: A second whole otolith age was determined by reader A to determine within-reader variability for *S. diploproa* and between-reader variability for *S. pinniger* (reader B had left this laboratory). The otoliths were sent to the Northwest and Alaska Fisheries Center (Seattle, Wash.) for an additional whole otolith age to determine between-agency variability. The otolith was dried, weighed, measured, and sectioned as described above; a single otolith section age for each specimen was determined by reader A for both species. Model-estimated ages were determined by use of the multiple regression models described below.

Data Analysis

Generally, data were recorded in a standard format and stored on the Oregon State University Cyber 70 computer. Data management and analysis were assisted by use of the Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975).

From the calibration subsample of otoliths, predictive regression equations were developed to estimate age from otolith morphometrics. Multiple regression models were fitted in the following form:

$$\text{Age} = b_1X_1 + b_2X_2 + b_3X_3 + b_nX_n + c$$

where age (years) is determined by conventional methods, b_n 's = regression coefficients, X_n 's = independent variables, and c = constant. Models were developed for males and females separately within each species with both otolith section ages and whole otolith ages as dependent variables.

Independent variables included otolith weight, otolith length, otolith width, the respective square and cubic terms of each, and the interaction variables (otolith weight/otolith length and otolith length/otolith width). With the exception of otolith weight, where both weight and the cube of weight were used as independent variables, square or cubic terms were not used if the raw values were entered. This decreased problems of multicollinearity. Models were fitted in a forward stepwise manner (Nie et al. 1975) with the inclusion level for independent variables set at $P = 0.10$.

The 1980 confirmation subsample was used to verify the models. Direct comparisons between ages determined for the same otoliths but different reading methods were accomplished by paired t -tests. Since age is not known with certainty for any otolith, the ages determined by reader A for *S. diploproa* and by reader B for *S. pinniger*, which were used to calibrate the models in the calibration subsample, were considered as "standard age". To conduct multiple comparisons of variability, deviations from standard age were defined as follows: "model-induced variation" is the difference between the standard age and the model-predicted age; "within-agency variation" is the difference between ages determined by reader A for *S. diploproa* and between readers A and B for *S. pinniger*; "between-agency variation" is the difference between the standard age and the age determined by the National Marine Fisheries Service (NMFS). A one-way analysis of variance (ANOVA) was used to compare these deviations. Multiple range testing was conducted using the least significance difference method with $\alpha = 0.05$. This analysis was conducted only for whole otoliths since only a single section age was determined on the 1980 confirmation subsample.

RESULTS

Sebastes diploproa

Locations of the collections of *S. diploproa* are shown in Figure 2; this species was taken from lat. 36°49' to 48°47' N and over a depth range of 62 to 338 m. The distribution was similar to that noted in 1977 (Boehlert 1980). A total of 975 male and 1,145 female specimens were taken during the survey. The length frequencies show a mode near 23 cm for males and 24 cm for females with secondary modes at 26 and 27 cm, respectively. Corresponding age frequencies (based upon whole

otoliths) show a clear mode at 7 yr for both males and females, with whole otolith age ranges from 1 to 46 for males and 0 to 55 for females. Mean lengths-at-age for males and females are similar until age 8, after which females grow more rapidly (Boehlert 1980; Boehlert and Kappenman 1980).

Subsampling every fourth pair of otoliths from all collections of *S. diploproa* resulted in 290

female and 246 male specimens. The subsample was representative of the latitudinal distribution, age range, and length range of the whole collection. Capture, otolith, and age data from these samples are summarized in Table 1. Otolith section ages, as expected, were typically greater than whole otolith ages (Table 1); this was particularly true at greater lengths. Correlation matrices of pertinent otolith and age data (Table 2) show that otolith weight has the strongest linear association with otolith section age; both otolith weight and age are exponential functions of fish length. Plotting otolith length, fish length, and otolith weight against otolith section age demonstrates the pattern of otolith growth (Fig. 3). Past an age of about 25 yr, both otolith length and fork length reach approximate asymptotes, whereas otolith weight continues to increase. The wide fluctuations in otolith weight apparent at older ages correlate closely with changes in fork length (Fig. 3); for this reason, otolith weight alone is a relatively poor predictor of fish age at greater ages where fork length is highly variable. Addition of otolith

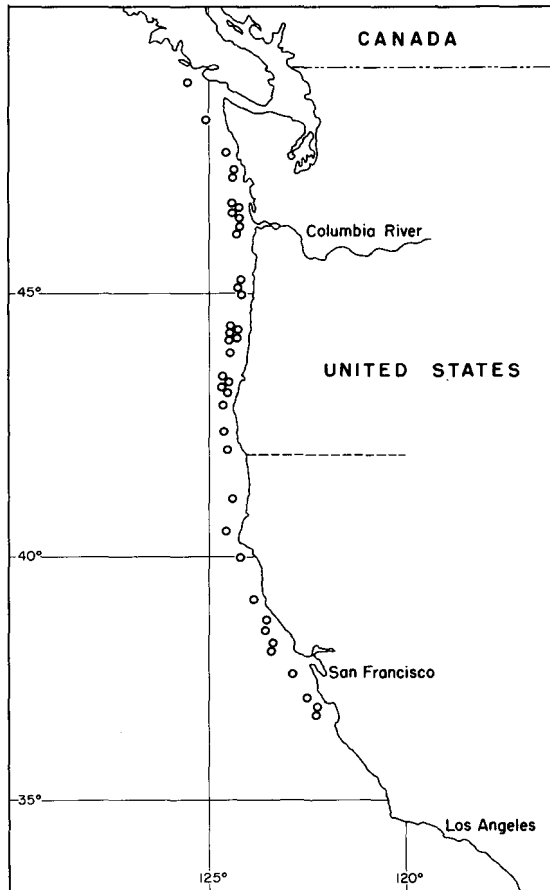


FIGURE 2.—Locations of 1980 West Coast Survey collections from which otoliths of *Sebastes diploproa* were taken.

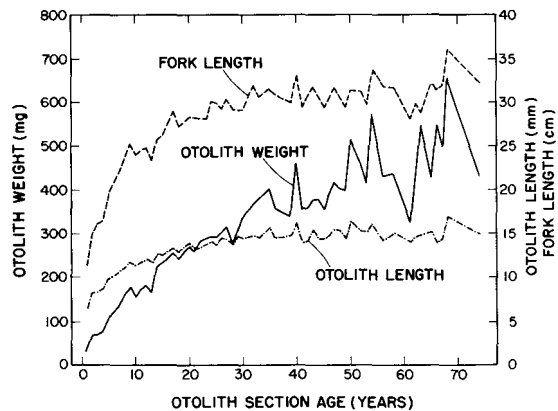


FIGURE 3.—Otolith characteristics of male *Sebastes diploproa* from the calibration subsample as related to fish length and age. $N = 246$. Note the covariation among the three curves, particularly at older ages.

TABLE 1.—Summary of biological and otolith data from the subsampled groups of *Sebastes diploproa* used in developing the age models.

Variable	Females ($N = 290$)				Males ($N = 246$)			
	Minimum	Maximum	Mean	SD	Minimum	Maximum	Mean	SD
Depth of capture (fathoms)	34	185	137	29.36	53	185	136	28.45
Fork length (mm)	130	378	264	56.16	94	364	246	48.19
Otolith length (mm)	7.71	18.02	12.49	2.35	5.47	17.03	11.82	2.14
Otolith width (mm)	5.08	11.25	7.97	1.31	3.59	10.32	7.57	1.14
Otolith thickness (mm)	0.83	2.97	1.41	0.44	0.73	2.84	1.35	0.39
Otolith dry weight (mg)	59	724	244.6	150.4	25	659	208	117.4
Whole otolith age (yr)	1	56	15.2	11.97	1	40	13.5	9.78
Otolith section age (yr)	2	66	17.2	15.68	1	74	16.9	16.41

TABLE 2.—Correlation matrix for selected otolith morphometric, weight, and age data for the calibration subsample of *Sebastes diploproa*.

	Otolith weight	Otolith length	Otolith width	Otolith thickness	Whole otolith age	Otolith section age
Females (<i>N</i> = 290)						
Fork length	0.912	0.969	0.956	0.766	0.862	0.819
Otolith section age	0.947	0.859	0.788	0.938	0.917	
Whole otolith age	0.925	0.893	0.837	0.901		
Otolith thickness	0.930	0.843	0.778			
Otolith width	0.893	0.948				
Otolith length	0.940					
Males (<i>N</i> = 246)						
Fork length	0.895	0.971	0.959	0.815	0.835	0.769
Otolith section age	0.938	0.807	0.710	0.905	0.907	
Whole otolith age	0.923	0.885	0.778	0.846		
Otolith thickness	0.903	0.778	0.725			
Otolith width	0.857	0.778				
Otolith length	0.922					

length and the interaction variables compensate for these changes in the pattern of otolith weight in the multiple regression models of fish age.

The multiple regression models relating fish age with otolith data were fitted with both whole otolith age and otolith section age as dependent variables. Independent variables included in the whole otolith age models, their coefficients, and significance levels are presented in Table 3. All coefficients were highly significant and the models explain 88.1% of the variation in age for females and 92.0% for males, as measured by the coefficient of determination, R^2 . Residuals from the models by age category show no trend up to age 35 for females and age 30 for males, after which there is a trend of increasing positive deviation with increasing age. The ages included in this part of the model, however, represented only 7.7% of female and 8.6% of male *S. diploproa* and are therefore not of great concern. These deviations are positive, however, suggesting that the model predictions may relate to otolith growth patterns which are more indicative of otolith section ages.

Variables included in the otolith section age models, their coefficients, standard errors, and significance levels are presented in Table 4. Again, all coefficients are highly significant, but the coefficients of determination are slightly less, explaining 86.1% of the variation in age for females and 85.0% for males. Mean residuals for the different age categories show no significant trend with age.

The model based upon whole otolith ages suffers from inaccuracies in the older ages, where otolith section ages are much greater than whole otolith ages. This is demonstrated in the trend of increasing residuals with increasing age. The model based upon otolith section age, however, is charac-

TABLE 3.—Regression coefficients and associated statistics on the multiple regression models of whole otolith age for *Sebastes diploproa*.

Variable	Coefficient	SE	<i>P</i>
Females (<i>N</i> = 290)			
Otolith weight	0.1343	0.0091	<0.001
(Otolith weight) ³	-0.107×10^{-6}	0.14×10^{-7}	<0.001
Otolith width	-2.558	0.571	<0.001
Constant (a)	6.4303	3.004	0.033
SD = 4.15			
Multiple correlation, <i>R</i> = 0.939			
Males (<i>N</i> = 246)			
Otolith weight	0.2179	0.0145	<0.001
(Otolith weight) ³	-0.1945×10^{-6}	0.14×10^{-7}	<0.001
Otolith width	-3.4542	0.3942	<0.001
Otolith weight/length	-1.0997	0.2402	<0.001
Constant (a)	16.2572	2.2186	<0.001
SD = 2.797			
Multiple correlation, <i>R</i> = 0.959			

TABLE 4.—Regression coefficients and associated statistics on the multiple regression models of otolith section age for *Sebastes diploproa*.

Variable	Coefficient	SE	<i>P</i>
Females (<i>N</i> = 290)			
Otolith weight	0.2270	0.0137	<0.001
(Otolith width) ²	-0.3288	0.0377	<0.001
(Otolith weight) ³	-0.1134×10^{-6}	0.155×10^{-7}	<0.001
(Otolith length) ²	-0.1114	0.0205	<0.001
Constant (a)	5.0243	1.2982	<0.001
SD = 4.232			
Multiple correlation, <i>R</i> = 0.928			
Males (<i>N</i> = 246)			
Otolith weight	0.2496	0.0158	<0.001
Otolith width ³	-5.7233	0.6949	<0.001
(Otolith weight) ³	-0.1315×10^{-6}	0.266×10^{-7}	<0.001
(Otolith length) ²	-0.0882	0.0256	<0.001
Constant (a)	23.540	3.3823	<0.001
SD = 4.620			
Multiple correlation, <i>R</i> = 0.922			

terized by slightly lower multiple correlation coefficients (Table 4). This may be a result of inaccuracies in estimates of otolith section age of younger fish, where greater difficulty in age de-

termination exists with sections. For this reason, I also constructed a hybrid multiple regression model based upon a combination of otolith section and whole otolith ages. The decision on which age to use was arbitrary in the following way: If the difference (otolith section age minus whole otolith age) was ≤ 5 yr, whole otolith age was chosen; if the difference was > 5 yr, otolith section age was chosen. The resulting models are described in Table 5. Independent variables similar to those in the other two models were chosen, and the multiple correlation coefficients were greater in each case.

To analyze the precision of the models, subsamples of 50 male and 50 female *S. diploproa* were taken from the remaining samples not used in the calibration subsample. Lengths and ages were representative of the respective ranges in the overall collection. Ranges of whole otolith age, NMFS age (that from the other agency), and otolith section age in these samples were 2-50, 3-49, and 2-75 for females and 3-34, 4-25, and 3-84 for males, respectively.

Whole otolith age was predicted based upon the appropriate whole otolith age models. Values of estimated age, whole otolith age, and NMFS age as a function of length are plotted in Figure 4. The deviation of NMFS age from whole otolith age increases with increasing length for both males and females. Deviations from the first whole otolith age are presented in Figure 5. Model-induced variability is the difference between estimated whole otolith age and whole otolith age; between-agency variability is whole otolith age minus NMFS age; within-agency variability is the difference of two successive age determinations by

the same reader. Mean values of these sources of variation are presented in Table 6 for females and Table 7 for males. In both cases, the mean between-agency variability is greater than either model-induced or within-agency variability. One-way ANOVA demonstrates a significant difference among the three sources (Tables 6, 7). Multiple range testing (least significant difference, $\alpha = 0.05$), moreover, demonstrates that the means are significantly different for both females and males; the range tests suggest that within-agency and model-induced variability are equal and are both significantly less than the between-agency variability.

Only a single otolith section age was determined for specimens from the 1980 confirmation subsample. Ages were estimated from the multiple regression model of section age (Table 4) and compared with conventionally determined section age

TABLE 5.—Regression coefficients and associated statistics on the multiple regression models of age in *Sebastes diploproa*. The ages used for the calibration of these models are based upon either whole otoliths or otolith sections as described in the text.

Variable	Coefficient	SE	P
Females (N = 290)			
Otolith weight	0.2233	0.0135	<0.001
(Otolith width) ²	-0.2983	0.0403	<0.001
(Otolith weight) ³	-0.1244×10^{-6}	0.1685×10^{-7}	<0.001
Otolith length	-2.495	0.5084	<0.001
Constant (a)	17.7993	3.7339	<0.001
SD = 4.3967			
Multiple correlation, R = 0.962			
Males (N = 246)			
Otolith weight	0.2504	0.0157	<0.001
(Otolith width) ²	-0.3598	0.0549	<0.001
(Otolith weight) ³	-0.1272×10^{-6}	0.2800×10^{-7}	<0.001
Otolith length	-2.4123	0.6071	<0.001
Constant (a)	16.6069	3.9145	<0.001
SD = 4.7479			
Multiple correlation, R = 0.958			

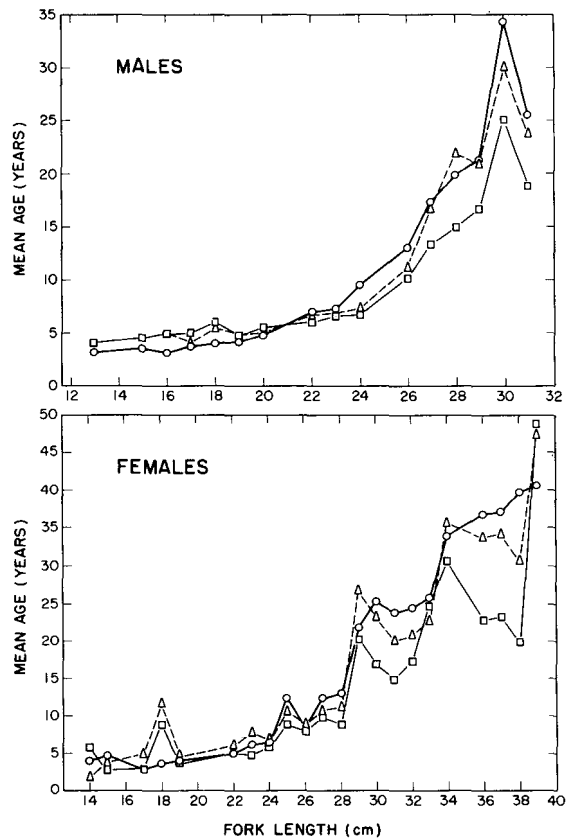


FIGURE 4.—Comparisons of mean whole otolith ages at length for the confirmation subsample of *Sebastes diploproa*. Triangles represent age from reader A, circles the age estimated by the model, and squares the age determined by another laboratory.

TABLE 6.—Results of one-way analysis of variance and multiple range tests comparing deviations of age from the standard age in *Sebastes diploproa* females. Group 1 = between-agency variability; group 2 = model-induced variability; group 3 = within-agency, within reader variability.

Source	df	Sum of squares	Mean squares	F	P
Analysis of variance					
Between groups	2	707.77	353.89	23.14	<0.001
Within groups	147	2,247.93	15.29		
Total	149	2,955.70			
Group	n	Mean	SD		
1	50	4.000	4.686		
2	50	-0.51	4.134		
3	50	-0.700	2.613		

Multiple range test (least significant difference, $\alpha = 0.05$)
Group 3 = Group 2 < Group 1

TABLE 7.—Results of one-way analysis of variance and multiple range tests comparing deviations of age from the standard age in *Sebastes diploproa* males. Group 1 = between-agency variability; group 2 = model-induced variability; group 3 = within-agency, within reader variability.

Source	df	Sum of squares	Mean squares	F	P
Analysis of variance					
Between groups	2	207.30	103.65	13.62	<0.001
Within groups	147	1,118.30	7.61		
Total	149	1,325.60			
Group	n	Mean	SD		
1	50	2.360	3.306		
2	50	0.108	2.294		
3	50	-0.320	2.575		

Multiple range test (least significant difference, $\alpha = 0.05$)
Group 3 = Group 2 < Group 1

(Fig. 6). Ages were close to those predicted from the model with the notable exception of the maximum age for both males and females. In each instance, the maximum ages were greater than the maximum otolith section age in the calibration subsample; the estimated section age is therefore an extrapolation from the model. For the overall subsample, however, the estimated section ages were not significantly different from those determined by conventional methods (paired *t*-test, $\alpha = 0.05$). The observed and predicted ages comparing the confirmation subsample with the predicted ages from the hybrid model are not presented graphically, but the form of the curves for both males and females is virtually identical to that for the section age model (Fig. 6).

Sebastes pinniger

Sebastes pinniger were collected from lat. 43°11' to 49°26'N at depths from 58 to 375 m (Fig. 7).

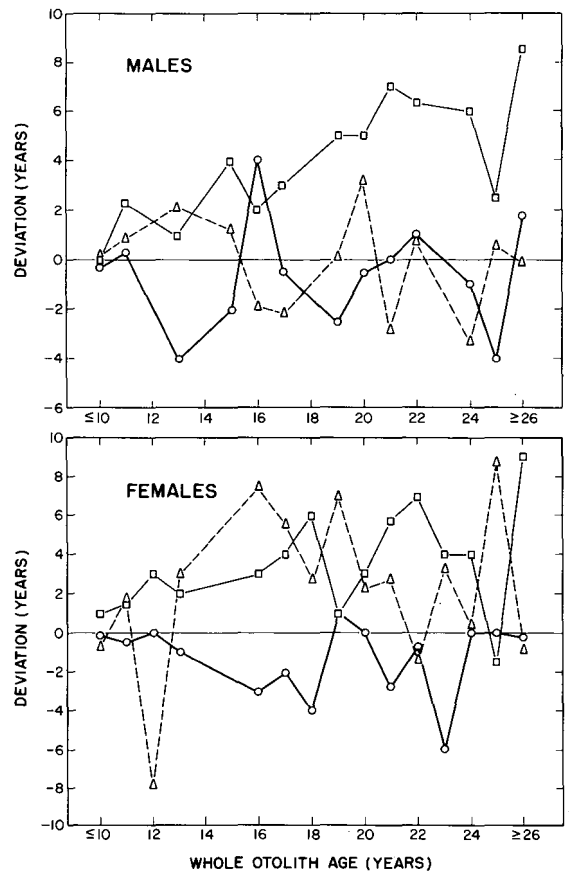


FIGURE 5.—Mean deviations of whole otolith ages from the confirmation subsample of *Sebastes diploproa*. Triangles represent model-induced variability, circles within-agency variability, and squares between-agency variability.

Pairs of otoliths from a total of 519 male and 369 female specimens were taken from the survey. Length frequencies for *S. pinniger* show a mode at 50 cm for males and 52 cm for females. Age frequencies of the entire sample (based upon whole otoliths) demonstrate a mode for both males and females at 12 to 13 yr. Whole otolith ages from the collections ranged from 2 to 25 for males and 2 to 22 for females.

Subsampling every third pair of otoliths from the whole collection resulted in 171 male and 121 female specimens of *S. pinniger*. Again, this subsample was representative of the latitudinal distribution, age range, and length range of the whole sample. Capture, otolith, and age data from these specimens are summarized in Table 8. Otolith section ages in larger fish are generally greater than whole otolith ages, but not to the

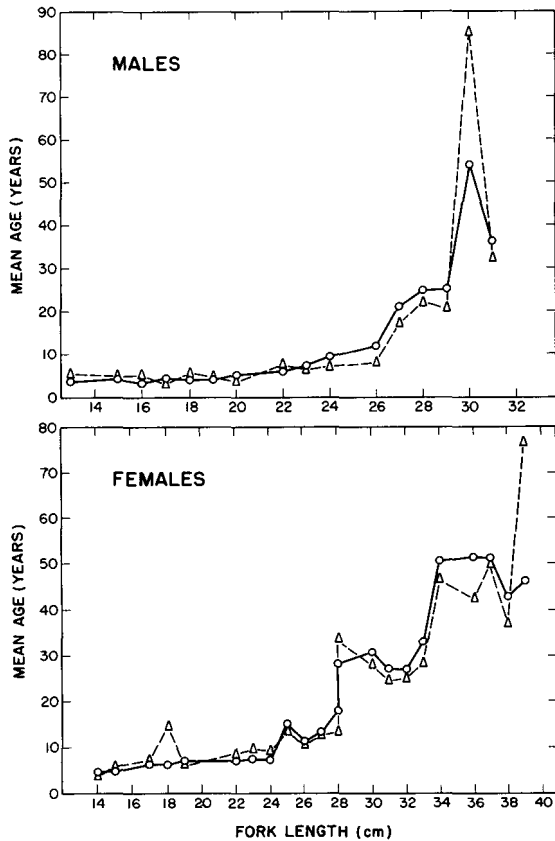


FIGURE 6.—Comparisons of mean otolith section ages at length from the confirmation subsample of *Sebastes diploproa*. Triangles represent otolith section age and circles the model estimated section age.

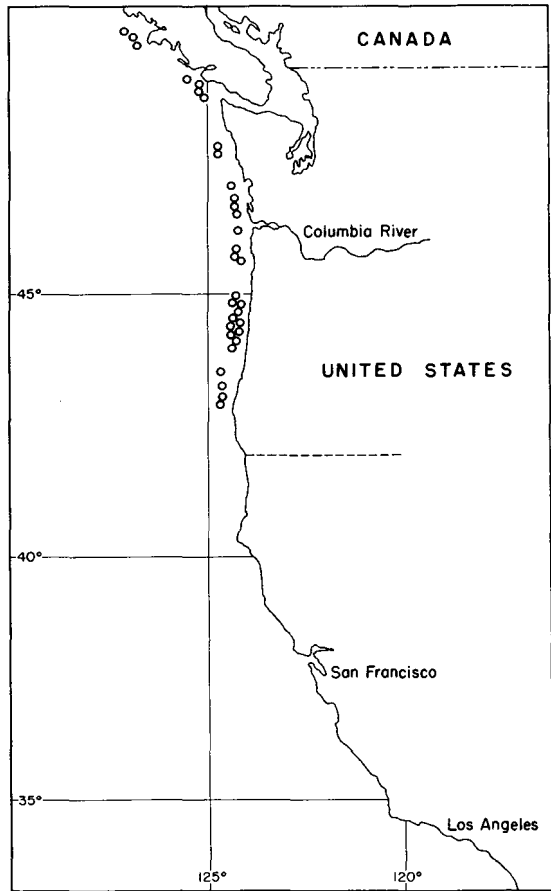


FIGURE 7.—Locations of 1980 West Coast Survey collections from which otoliths of *Sebastes pinniger* were taken for the current study. Samples from the FV *Pat San Marie* and the FV *Mary Lou* are included.

TABLE 8.—Summary of biological and otolith data from the subsampled groups of *Sebastes pinniger* used in developing the age models.

Variable	Females (N = 121)				Males (N = 171)			
	Minimum	Maximum	Mean	SD	Minimum	Maximum	Mean	SD
Depth of capture (fathoms)	32	100	69.8	12.66	37	103	73.3	14.39
Fork length (mm)	152	610	497.8	69.25	170	579	481.64	64.20
Otolith length (mm)	8.00	23.40	19.62	2.27	8.59	22.89	19.56	2.31
Otolith width (mm)	4.45	12.02	9.60	1.06	4.69	11.07	9.46	1.01
Otolith thickness (mm)	0.83	2.01	1.54	0.19	0.79	2.41	1.64	0.29
Otolith dry weight (mg)	53	821	486.7	135.5	58	867	517.0	160.69
Whole otolith age (yr)	2	19	12.4	3.16	2	25	13.2	3.79
Otolith section age (yr)	2	33	14.83	5.09	2	54	20.02	9.77

extent seen for *S. diploproa*. Otolith weight is again an exponential function of length, particularly for males. For females, however, this relationship was nearly linear. Of the ages determined in the calibration subsample, otolith weight has the strongest linear association with whole otolith

age for females and whole otolith age and section age for males (Table 9).

The multiple regression models constructed to predict whole otolith age were based upon fewer variables than for *S. diploproa*, but included variables were highly significant (Table 10). The coeffi-

TABLE 9.—Correlation matrix for selected otolith morphometric, weight, and age data for the calibration subsample of *Sebastes pinniger*.

	Otolith weight	Otolith length	Otolith width	Otolith thickness	Whole otolith age	Otolith section age
Females (N = 121)						
Fork length	0.915	0.948	0.923	0.779	0.895	0.755
Otolith section age	0.825	0.735	0.757	0.718	0.795	
Whole otolith age	0.890	0.887	0.851	0.756		
Otolith thickness	0.826	0.765	0.756			
Otolith width	0.920	0.902				
Otolith length	0.917					
Males (N = 171)						
Fork length	0.844	0.940	0.909	0.754	0.847	0.682
Otolith section age	0.898	0.694	0.696	0.883	0.809	
Whole otolith age	0.892	0.837	0.815	0.830		
Otolith thickness	0.910	0.769	0.750			
Otolith width	0.869	0.901				
Otolith length	0.879					

TABLE 10.—Regression coefficients and associated statistics on the multiple regression models of whole otolith age for *Sebastes pinniger*.

Variable	Coefficient	SE	P
Females (N = 121)			
(Otolith length) ³	0.00095	0.00011	<0.001
(Otolith width) ²	0.0448	0.0126	0.001
SD = 1.30			
Multiple correlation, R = 0.913			
Males (N = 171)			
Otolith weight	0.0280	0.00214	<0.001
(Otolith width) ³	-0.845 × 10 ⁻⁸	0.241 × 10 ⁻⁸	0.001
SD = 1.665			
Multiple correlation, R = 0.900			

cient of determination (R^2) suggests that the models of whole otolith age explain 83.4% of the variation in age for females and 81.0% for males. For both males and females, the constant in the regression was not significantly different from zero and was not included in the models. The residuals from the models show no distinct trend with the exception of a slight increase at ages >17 yr for males; this included 11.1% of the sample.

The variables included in the otolith section age models, their coefficients, standard errors, and significance levels are presented in Table 11. As in the whole otolith age models, there are fewer variables included than for *S. diploproa*; for the male section age model, for example, there is only one variable and the constant included for prediction of age. All variables are highly significant and the coefficients of determination suggest that the otolith section models explain 70.2% of the variation in age for females and 84.6% for males. Mean residuals show a strong trend of increase at ages past 26 yr for male otolith section age models; this represented 23% of the sample.

A model incorporating both otolith section age and whole otolith age was developed using the

same criteria for age as in *S. diploproa*. These models were based upon more independent variables but were not significantly better (as based upon the coefficient of determination) than the otolith section models (Table 12). Based upon the multiple correlation coefficients, the best models for *S. pinniger* would be the hybrid model for males and the whole otolith model for females.

For analyzing the precision of the models, sub-

TABLE 11.—Regression coefficients and associated statistics on the multiple regression models of otolith section age for *Sebastes pinniger*.

Variable	Coefficient	SE	P
Females (N = 121)			
(Otolith weight) ²	0.272 × 10 ⁻⁴	0.382 × 10 ⁻⁵	<0.001
Otolith width	0.8368	0.4586	0.071
SD = 2.80			
Multiple correlation, R = 0.838			
Males (N = 171)			
(Otolith weight) ²	0.546 × 10 ⁻⁴	0.179 × 10 ⁻⁵	<0.001
Constant (a)	4.0297	0.6022	<0.001
SD = 3.85			
Multiple correlation, R = 0.920			

TABLE 12.—Regression coefficients and associated statistics on the multiple regression models of age in *Sebastes pinniger*. The ages used for the calibration of these models are based upon either whole otoliths or otolith sections as described in the text.

Variable	Coefficient	SE	P
Females (N = 121)			
(Otolith weight) ²	0.2621 × 10 ⁻⁴	0.4518 × 10 ⁻⁵	0.001
(Otolith width) ³	0.4038 × 10 ⁻²	0.2186 × 10 ⁻²	0.067
Constant (a)	3.2137	1.1296	0.005
SD = 2.8239			
Multiple correlation, R = 0.840			
Males (N = 171)			
(Otolith weight) ²	0.1306 × 10 ⁻³	0.2359 × 10 ⁻⁴	<0.001
(Otolith length) ³	-0.2044 × 10 ⁻²	0.5456 × 10 ⁻³	<0.001
(Otolith weight) ³	-0.6026 × 10 ⁻⁷	0.2197 × 10 ⁻⁷	0.007
Otolith length/width	9.7349	4.1381	0.020
Constant (a)	-12.8239	7.4064	0.085
SD = 3.9989			
Multiple correlation, R = 0.924			

samples of 50 male and 50 female *S. pinniger* were taken from the remaining 1980 samples not used in the calibration subsample. These subsamples were representative of the length and age ranges in the overall collection. Ranges of whole otolith age, NMFS age, and otolith section age in these subsamples were 4-26, 4-25, and 4-29 for females and 7-35, 7-32, and 8-45 for males, respectively.

Whole otolith age was estimated from the appropriate whole otolith age model for males and females. Values of model estimated age, whole otolith age, and NMFS age as a function of length are plotted in Figure 8. Female *S. pinniger* ages are similar for all three age determination methods. For males, model-estimated age is similar to the whole otolith age but both are less than the NMFS age (Fig. 8). Deviations from the whole otolith age by the otolith reader whose ages were used to calibrate the model are shown in Figure 9.

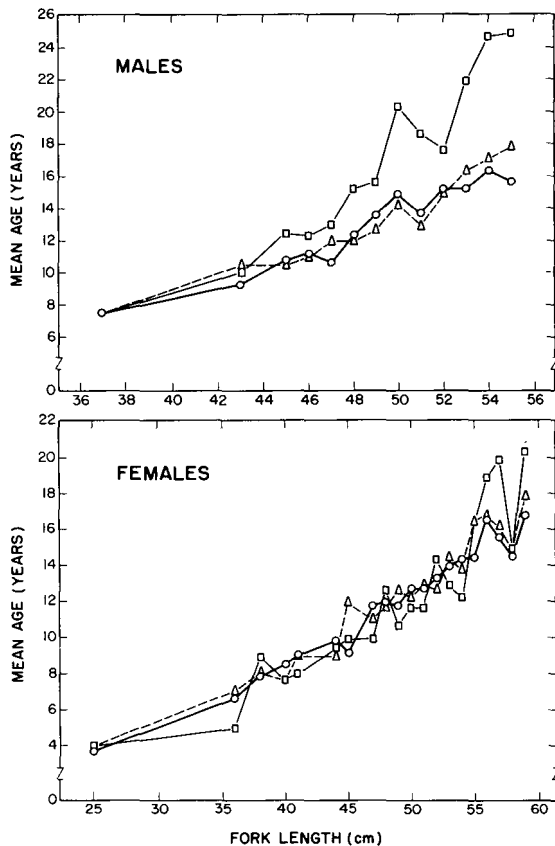


FIGURE 8.—Comparisons of mean whole otolith ages at length from the confirmation subsample of *Sebastes pinniger*. Triangles represent age from reader B, circles the age estimated by the model, squares the age determined by another laboratory.

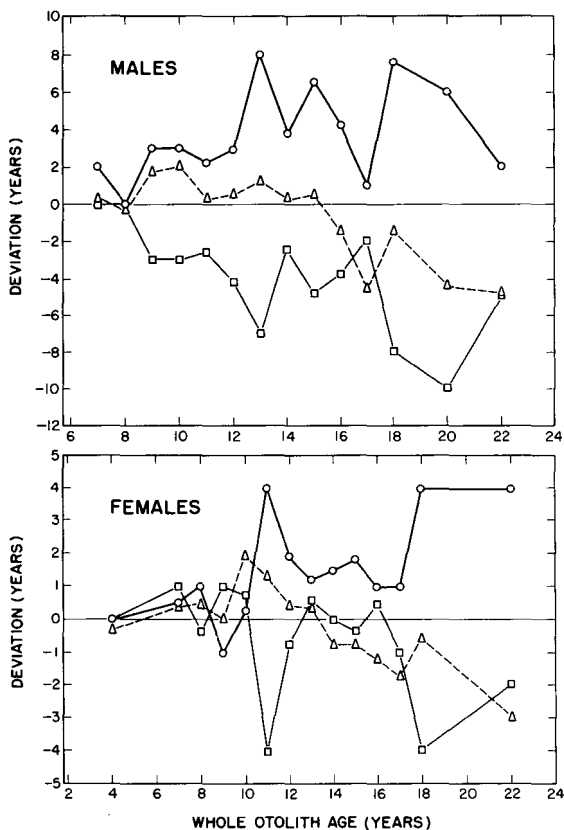


FIGURE 9.—Mean deviations of whole otolith ages from the confirmation subsample of *Sebastes pinniger*. Triangles represent model-induced variability, circles within-agency variability, and squares between-agency variability.

The explanation of these deviations is the same as for *S. diploproa* with the exception that the within-agency variability is a between-reader rather than a within-reader variability. One-way ANOVA within these deviations shows significant differences among the groups for both females (Table 13) and males (Table 14). Multiple range testing (least significant difference, $\alpha = 0.05$) demonstrates that for females, mean between-agency variability and model-induced variability are equal but are both less than within-agency variability (for *S. pinniger* this was based upon two different readers). For males, between-agency variability is less than model-induced variability which is less than within-agency variability. For the purposes of this comparison, however, the model-induced variability is significantly closer to zero than either of the other sources of variability (Table 14).

In the confirmation subsample, section ages estimated from the multiple regression model are

TABLE 13.—Results of one-way analysis of variance and multiple range tests comparing deviations of age from the standard age in *Sebastes pinniger* females. Group 1 = between-agency variability; group 2 = model-induced variability; group 3 = within-agency, between reader variability.

Source	df	Sum of squares	Mean squares	F	P
Analysis of variance					
Between groups	2	88.69	44.34	8.67	<0.001
Within groups	147	751.84	5.11		
Total	149	840.53			
Group	n	Mean	SD		
1	50	-0.320	2.817		
2	50	-0.021	1.516		
3	50	1.44	2.260		

Multiple range test (least significant difference, $\alpha = 0.05$)
Group 1 = Group 2 < Group 3

TABLE 14.—Results of one-way analysis of variance and multiple range tests comparing deviations of age from the standard age in *Sebastes pinniger* males. Group 1 = between-agency variability; group 2 = model-induced variability; group 3 = within-agency, between reader variability.

Source	df	Sum of squares	Mean squares	F	P
Analysis of variance					
Between groups	2	1,840.42	920.21	67.43	<0.001
Within groups	147	2,006.21	13.65		
Total	149	3,846.63			
Group	n	Mean	SD		
1	50	-4.280	4.427		
2	50	-0.111	2.107		
3	50	4.300	4.112		

Multiple range test (least significant difference, $\alpha = 0.05$)
Group 1 < Group 2 < Group 3

compared with conventional section ages in Figure 10. The two ages are similar and as a whole are not significantly different for females but are significantly different for males (paired t -test, $\alpha = 0.05$). This is presumably a result of the consistently overestimated otolith section age for *S. pinniger* males. The ages estimated from the hybrid model (Fig. 11) are not significantly different from those determined by the appropriate conventional age (paired t -test, $\alpha = 0.05$).

DISCUSSION

The results of this research demonstrate the potential for using objective criteria and multivariate models to determine age in fast- and slow-growing members of the genus *Sebastes*. Past studies have used weight of the eye lens for estimates of age in fishes, amphibians, and certain mammals (Crivelli 1980; Malcolm and Brooks 1981). In fishes, however, this technique is only

good for fast-growing species and provides poor estimates of age after several years when length at age becomes highly variable (Crivelli 1980); the same problems exist in estimating age from modal lengths. Growth of most body parts, including the eye lens, is allometric with length rather than age. Growth of the otolith, however, as described above, is a complex function of age as well as length. After a certain size is reached, the fish otolith does not increase in length or width, but continues to increase in thickness, and therefore weight, with age (Fig. 3). The increasing thickness is a function of addition of aragonite crystals only on the internal surface of the otolith (Fig. 1).

Similar patterns of otolith growth in length, width, thickness, and weight have been observed

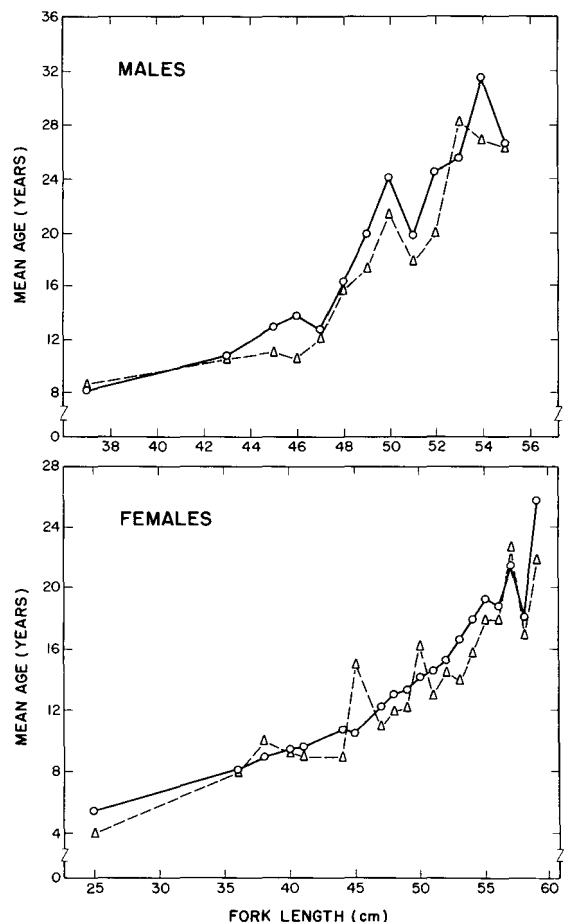


FIGURE 10.—Comparisons of mean otolith section ages at length from the confirmation subsample of *Sebastes pinniger*. Triangles represent otolith section age and circles the model estimated section age.

in other species of fish, but the information has not been applied to the estimation of age, with the exception of preliminary tests using discriminant techniques by Brander (1974). Templeman and Squire (1956), however, noted the importance of this information: "In many fishes, in which accurate age reading is doubtful, otolith weights, which are more factual, may offer a better separation of fish populations than growth rates which are dependent on the judgement of the scale- or otolith-reader." Weight and otolith measurements are valid criteria for age determination based upon the models (Tables 3-5, 10-12) and provide good estimates of age compared with other reading methods (Tables 6, 7, 13, 14; Figs. 4-6, 8-11). Based upon published patterns of otolith growth, these techniques should work for other species of *Sebastes* (Sandeman 1961; Beamish 1979b), Pacific hake (Beamish 1979a), haddock (Templeman and Squire 1956), plaice, sole, turbot, and horse mackerel (Blacker 1974a), and cod (Trout 1954; Blacker 1974a), among others. This technique may therefore be amenable to a wide variety of species of fishes.

Ages determined by scale or otolith readers are generally based on subjective decisions by the age reader, who reads annuli but must distinguish from "false checks", "metamorphic checks", and "spawning checks" (Trout 1961; Bailey et al. 1977).

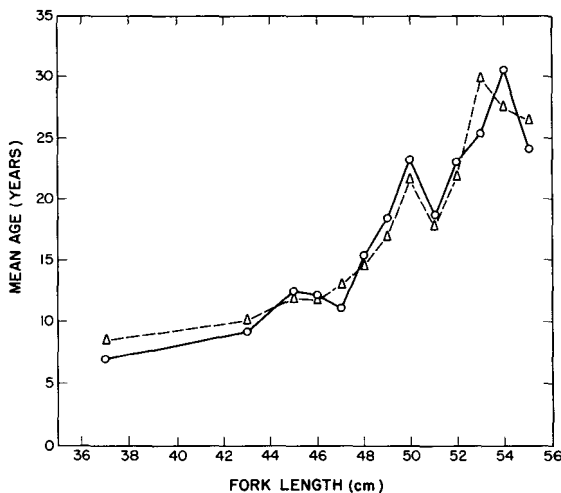


FIGURE 11. — Comparison of ages determined from otoliths and those predicted by the hybrid regression model for *Sebastes piniger* males. Otolith ages were based upon whole otolith ages if the difference between section and whole otolith ages were ≤ 5 ; otherwise, otolith sections were used. Triangles represent whole otolith or section age and squares the model estimated age.

With experience comes reduced individual variability, but aging variability among different otolith readers and especially among different agencies is great; such variability can have important effects upon the estimates of growth parameters important for fisheries management (Sandeman 1961; Brander 1974; Hirschhorn 1974; Kimura et al. 1979). While otolith or scale exchanges are occasionally made between agencies for calibration purposes, this represents additional time spent for gaining greater consistency in ages (Westrheim and Harling 1973; Blacker 1974b), and difficulties may remain if disagreement in aging techniques cannot be resolved. Blacker (1974a) noted that "Recent progress in the use of otoliths for age determination has been limited mainly to the development of new techniques for preparing otoliths for reading and for photography so that aging methods can be readily compared." The techniques described in the present study represent a new approach to the systematic and repeated age determination in species for which continued age determination is necessary; once calibrated and implemented, the models would reduce between-reader and between-agency variability in age determination. Further research, however, should be conducted on variations in the models over seasons, regions, and different years to determine to what extent repeated calibration is necessary.

Ancillary benefits of the proposed methodology include its simplicity. Reliable, repeatable estimates of age require a great deal of experience on the part of an otolith or scale reader using conventional aging methodology (Blacker 1974a). It is often difficult to maintain a staff of trained otolith readers and retraining may require a large time commitment. The techniques described here require no special training, since the criteria (otolith length, otolith width, and otolith dry weight) are objective and can be measured with simple dial calipers and balance. Time expended for age determination by different methods is as follows: An experienced otolith reader averages about 17 ages/h on whole otoliths, but only 6 to 8 ages/h when otolith sections are used due to the additional preparation necessary. An untrained technician, however, can determine the measurements necessary for the model-based age estimates at a rate of about 40 otoliths/h on a long-term basis. Since the criteria for age are measurable, the techniques will be amenable to automation. Several attempts have been made in the past to automate or semiautomate age analysis using imaging

systems based upon differential light transmission (Fawell 1974; Mason 1974). These techniques have generally not been implemented, however, due to the subjective and variable nature of the criteria. Implementation of these techniques with automated systems could result in even further savings of time.

Since estimating the age distribution of exploited fish populations remains an important part of fishery biology, new and improved techniques of age determination are desirable. For shorter lived species, length-based methods are proving important (Pauly and David 1981). Age-length keys are also used quite extensively. Sample sizes necessary for accurate age-length keys, however, must be quite large, particularly for long-lived species such as *Sebastes*. In my relatively small calibration subsamples, for example, there are up to 15 age classes in a single 1 cm length interval (Table 15). Considering the

TABLE 15.—Number of age classes within single 1 cm length intervals from the calibration subsample. *N* = number of *Sebastes* specimens in the subsample.

Species	Sex	<i>N</i>	Whole otolith age	Otolith section age
<i>S. diploproa</i>	Female	290	14	14
	Male	246	12	14
<i>S. pinniger</i>	Female	121	6	11
	Male	171	9	15

maximum age of *S. diploproa* (Bennett et al. 1982), there could potentially be up to 50 age classes in a single length interval if a sufficient sample size were taken. For such species, age-length keys will be difficult to extrapolate meaningfully to the entire population without very large sample sizes, which must accordingly be aged. Similar, but more severe, problems will apply to techniques which attempt to extract growth parameters from length-frequency data for such long-lived species. The techniques developed by Pauly and David (1981) for faster growing species would be complemented by the current technique for slow-growing, difficult-to-age species. Otoliths could be collected by station, sex, and species without regard to size. From each otolith, after calibration of an age model, the available information could include both fish length and age. This approach to length data collection is not new and has been used by the International Pacific Halibut Commission for several years to estimate length (Southward 1962; Quinn et al. 1983). These techniques could therefore streamline not only the collection of

otoliths at sea but also the analysis of age in the laboratory.

The difficulty in age determination described above and the resulting variability between laboratories may have a negative impact upon accuracy of fishery models, particularly those using cohort or virtual population analysis (Brander 1974; Alverson and Carney 1975). The new methodology can provide significant time and cost savings over conventional methods and also decrease variability in age estimates. Implementation of these aging techniques, however, will require careful calibration with ages determined by a consensus of expert otolith readers from all management agencies with an interest in each species for which a model is developed.

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