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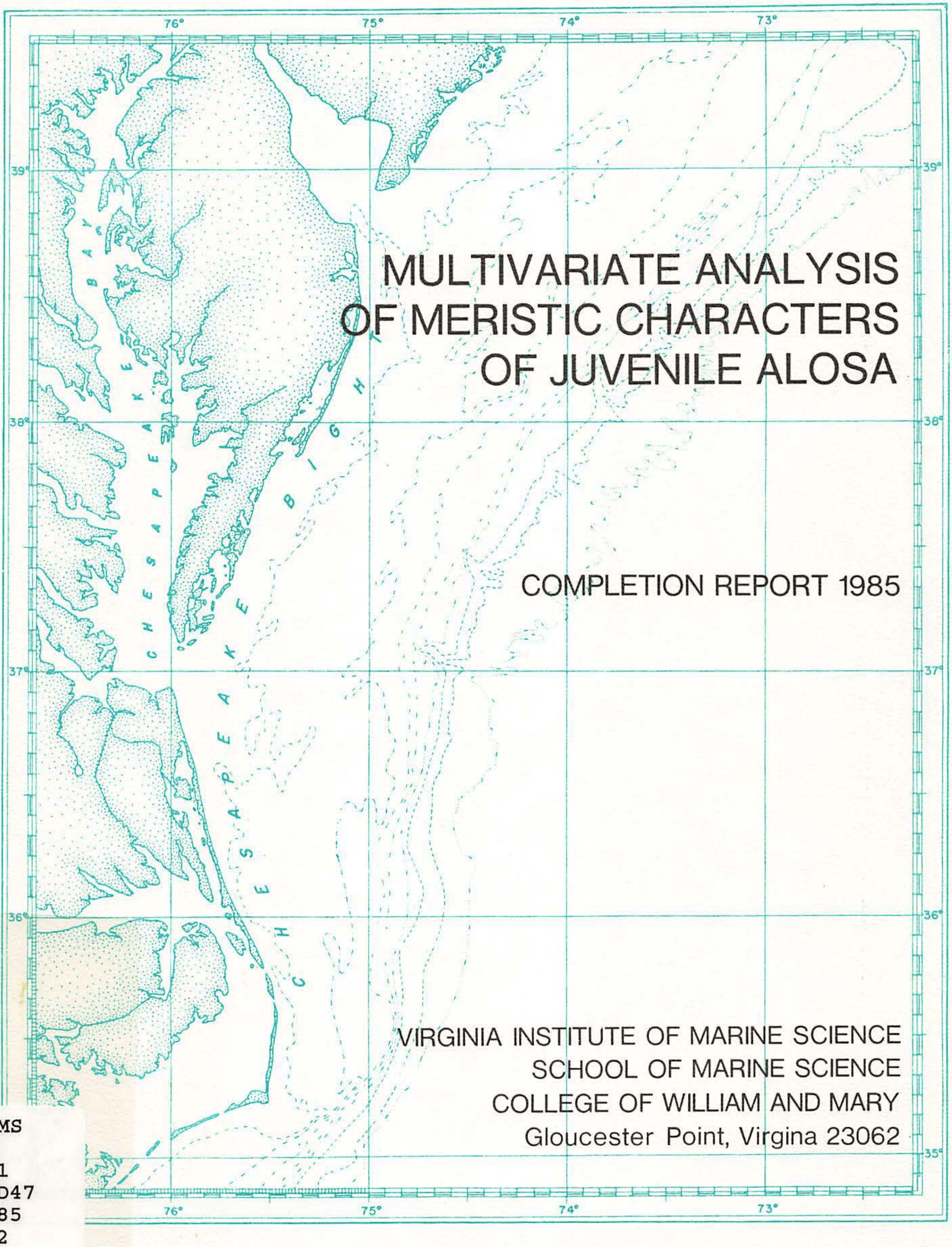

MULTIVARIATE ANALYSIS OF MERISTIC CHARACTERS OF JUVENILE ALOSA

COMPLETION REPORT 1985

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1. SUMMARY

The objective was to determine if meristic studies supported a premise of river-specific stocks of American shad (Alosa sapidissima), alewife (A. pseudoharengus) and blueback herring (A. aestivalis) in Chesapeake Bay. Information gathered from this study will add to the general body of data gathered for the implementation of management plans for each species.

Specimens were collected from the Potomac, Rappahannock, Mattaponi, Pamunkey, and James Rivers from 1978 to 1980. The meristic characters examined were: dorsal, anal, left pectoral and left ventral rays, anterior and posterior scutes, and the total number of scutes.

Regression analysis indicated that each meristic character was independent of total length. A factorial multivariate analysis of variance (MANOVA) of American shad meristics indicated a significant difference among years, but the area differences and the area-year interactions were nonsignificant. The MANOVA analyses for alewife and blueback herring meristics indicated significant differences for both main effects (area and year), but these results were not interpretable because the area-year interactions were also significant. The alewife and blueback herring MANOVA analyses of simple effects also indicated that years were significantly different in each area, and areas were significantly different in each year. Thus, the characters used in this study are very plastic. We conclude that the meristic study does not support a premise of separate American shad stocks in the Mattaponi and Pamunkey Rivers, nor river-specific stocks of alewife and blueback herring in Chesapeake Bay.

2. INTRODUCTION

American shad (Alosa sapidissima) are reported to return to their natal streams to spawn on the basis of meristic studies (Vladykov and Wallace 1938; Warfel and Olsen 1947; Fischler 1959; Hill 1959; Nichols 1966), life history characteristics (Walburg and Nichols 1967; Leggett 1969; Carscadden and Leggett 1975) and tagging studies (Hollis 1948; Talbot and Sykes 1958). On the basis of a discriminant function analysis of meristic characters, Messieh (1977) suggested that alewife (A. pseudoharengus) and blueback herring (A. aestivalis) homed, but there was a high degree of straying from natal tributaries in the St. John River, New Brunswick.

A relationship between the latitudinal distribution of some fishes and the number of fin rays and other meristic characters has been shown, with counts of meristic characters increasing to the north (Hubbs 1926; Vladykov 1934; Tåning 1952; Barlow 1961). The number of serial elements (fin rays, scutes, etc.) are apparently determined by developmental rate (Garside 1966) which in turn is related to water temperature (Tester 1938; Lindsey 1954), and possibly other factors such as dissolved oxygen and salinity. Tåning (1952) determined that the number of fin rays and vertebral centra were fixed in a relatively short period of time during early development that he called the "sensitive period". Tester (1938) studied Pacific herring (Clupea palasii) and showed that vertebral count was inversely proportional to water temperature. In a meristic study of Pacific herring, McHugh (1954) reported that the number of anal and pectoral rays, and the number of scutes increased from south to north. Additionally, he stated that there was a general conclusion among researchers that the number of vertebrae and meristic characters increase from south to north, although the cline may be irregular and samples from adjacent areas may differ greatly.

The objective herein was to determine if meristic studies supported a premise of river-specific stocks of alosids in Chesapeake Bay. This study was supported by funds from the National Marine Fisheries Service, Northeast Section, Gloucester, Massachusetts.

3. MATERIALS and METHODS

3.1 SAMPLING

Juvenile (young-of-the-year) alewife, blueback herring and American shad were collected in 1978, 1979 and 1980 from five tributaries to Chesapeake Bay (Fig. 1). Samples were obtained with a pushnet (Kriete and Loesch 1980) at night when the juveniles are more accessible in surface waters (Loesch et al. 1982). Juveniles, rather than adults, were chosen to work with in order to ensure both the singularity of age and origin. The systems sampled were the Potomac, Rappahannock, Mattaponi, Pamunkey, and the James Rivers.

All samples were preserved in 10% buffered formalin at the time of capture and returned to VIMS to be sorted. After sorting by species, the samples were transferred to 40% isopropyl alcohol for storage. Random subsamples of 50 (as available) were drawn from each sample for analysis, and examined with a binocular dissecting microscope.

3.2 CHARACTERS EXAMINED

Meristic characters examined were dorsal (DR), anal (AR), left pectoral (PR), and left ventral (VR) rays, and anterior (AS) and posterior (PS) scutes. Total scute counts were correlated to AS and PS, and thereforeomitted from statistical analysis. All counts were made in the manner described by Hubbs and Lagler (1964) with the last two bases of the dorsal and anal fin rays counted as one. To make the distinction between anterior and posterior scutes, Reed's (1964) method was followed, where all scutes having their bases anterior to the insertion of the ventral fins were designated as anterior scutes. Posterior scutes were those with their bases posterior to the insertion of the ventral fins. All counts were made with a binocular dissecting scope and repeated for accuracy. Total fish length (TL) was measured to the nearest 0.1 mm with dial calipers.

3.3 STATISTICAL ANALYSIS

Regression analysis was used to determine if the chosen characteristics were independent of total length. Univariate descriptive statistics (mean, mode, standard deviation, and the frequency distribution) were calculated for each character in each sample. The descriptive statistics were used for insight, but not for statistical inference.

A factorial multivariate analysis of variance (MANOVA) was used to test for significant differences in meristic centroids (in k=6 space) among the main effects (area and year), interactions (area-year), and simple effects (areas within each year, and years within each area). The packaged program MANOVA from SPSS^X (1983) was used in these analyses and run on the VIMS PRIME 850 computer. The Wilks' criterion was used to examine the hypotheses. No juvenile American shad or alewife were collected in the James River in 1979 and 1980. Also, no juvenile American shad were captured in the Potomac and Rappahannock Rivers in any of the three years. The American shad MANOVA was therefore limited to the Mattaponi and Pamunkey

Rivers, and the alewife MANOVA excluded the James River. The MANOVA model was complete (in a statistical sense) for blueback herring, but incomplete and unbalanced for alewives because none were obtained in 1979 from the Mattaponi River, and replications were unequal. The American shad model was incomplete because of the absence of a 1980 sample for the Mattaponi River.

4. RESULTS

4.1 DESCRIPTIVE STATISTICS

4.1.1 ALEWIFE

Subsamples of 571 juvenile alewives collected from the Potomac, Rappahannock and Pamunkey Rivers in 1978, 1979 and 1980, from the Mattaponi River in 1978 and 1980, and from the James River in 1978 were examined (Table 1).

DORSAL RAYS

Counts and means of dorsal rays ranged from 16 to 19 and 16.82 to 17.82, respectively (Table 2). The Pamunkey subsamples consistently had the highest annual mean value, but its modal value, like those for the other rivers, was not constant, alternating between 17 and 18.

ANAL RAYS

Counts and means of anal rays ranged from 15 to 21 and from 17.78 to 18.70, respectively (Table 2). Modal values ranged from 18 to 19, but the value was constant (18) only for the Mattaponi and Pamunkey juveniles.

PECTORAL RAYS

Counts and means of pectoral rays ranged from 12 to 16 and 14.13 to 15.14, respectively (Table 2). Subsamples from the Rappahannock River had the highest mean values for each year while the Pamunkey River subsamples had the lowest. Modal values ranged from 14 to 15, but was constant only in the Rappahannock (15) and Mattaponi (14) juveniles.

VENTRAL RAYS

Counts and means of ventral rays ranged from 7 to 10 and 8.88 to 9.04, respectively (Table 2). Ventral rays was one of only two characters that had a constant mode (9).

ANTERIOR SCUTES

Counts and means of anterior scutes ranged from 17 to 22 and 18.70 to 19.32, respectively (Table 2). Anterior scutes was the only character other than ventral rays, that exhibited a constant mode (19).

POSTERIOR SCUTES

Counts and means of posterior scutes ranged from 12 to 17 and 14.02 to 14.91, respectively (Table 2). Modal values ranged from 14 to 15, but the value was constant only for the Rappahannock, Mattaponi and Pamunkey juveniles.

TOTAL SCUTES

Counts and means of total scutes ranged from 31 to 36 and 33.20 to 34.00, respectively (Table 2). All modal values were 34, with the exception of the 1979 and 1980 values for juveniles from the Potomac River.

4.1.2 BLUEBACK HERRING

Subsamples of 750 juvenile blueback herring collected from each of the five rivers in 1978, 1979 and 1980 were examined (Table 3).

DORSAL RAYS

Counts and means of dorsal rays ranged from 15 to 18 and 16.30 to 17.12, respectively (Table 4). The Mattaponi juveniles had the highest mean values each year. With the exception of the Potomac subsample in 1980, the modal value remained constant (17).

ANAL RAYS

Counts and means of anal rays ranged from 16 to 20 and 17.18 to 17.98, respectively (Table 4). Modal values were not constant for any of the subsamples, alternating between 17 and 18.

PECTORAL RAYS

Counts and means of pectoral rays ranged from 12 to 17 and 14.44 to 15.54, respectively (Table 4). Modal values were constant only in the James subsample (15), while the others alternated between 14, 15 and 16.

VENTRAL RAYS

Counts and means of ventral rays ranged from 8 to 10 and 8.96 to 9.08, respectively (Table 4). As with alewives, the modal values were constant (9).

ANTERIOR SCUTES

Counts and means of anterior scutes ranged from 18 to 22 and 19.66 to 20.84, respectively (Table 4). Unlike alewives, the modal values were not constant, shifting between 20 and 21.

POSTERIOR SCUTES

Counts and means of posterior scutes ranged from 12 to 17 and 13.74 to 15.24, respectively (Table 4). Modal values were 14 for all subsamples in 1978 and 1979, but shifted to 15 in 1980.

TOTAL SCUTES

Counts and means of total scutes ranged from 31 to 37 and 34.32 to 35.24, respectively (Table 4). Mean value was lowest in the Potomac subsamples each year. The modal values were constant (35), except for the occurrence of co-modality (34 and 35) in the Potomac subsample in 1978.

4.1.3 AMERICAN SHAD

Subsamples of 300 juvenile American shad taken from the Pamunkey River in 1978, 1979 and 1980, the Mattaponi River in 1978 and 1979, and the James River in 1978 were examined (Table 5).

DORSAL RAYS

Counts and means of dorsal rays ranged from 15 to 19 and 17.10 to 17.90, respectively (Table 6). Modal values were constant (17), except for the Pamunkey River juveniles in 1980.

ANAL RAYS

Counts and means of anal rays ranged from 17 to 22 and 19.46 to 20.54, respectively (Table 6). Modal values remained constant for the Mattaponi and Pamunkey River juveniles at 20, and the James River juveniles at 19.

PECTORAL RAYS

Counts and means of pectoral rays ranged from 15 to 20 and 15.64 to 16.52, respectively (Table 6). Modal values were not constant, alternating between 16 and 17.

VENTRAL RAYS

Counts and means of ventral rays ranged from 8 to 10 and 8.76 to 9.00, respectively (Table 6). Modal values remained constant (9), as was the case for alewife and blueback herring.

ANTERIOR SCUTES

Counts and means of anterior scutes ranged from 18 to 23 and 20.30 to 20.76, respectively (Table 6). Modal values were not constant, shifting between 20 and 21.

POSTERIOR SCUTES

Counts and means of posterior scutes ranged from 14 to 18 and 15.58 to 16.50, respectively (Table 6). Modal values ranged from 15 to 17, with co-modality (16 and 17) occurring in both the Pamunkey and James River juveniles in 1978.

TOTAL SCUTES

Counts and means of total scutes ranged from 34 to 39 and 36.34 to 37.06, respectively (Table 6). Modal values were constant (37) for all subsamples, except the Mattaponi River subsample in 1979 (36).

4.2 GENERAL COMMENTS

The descriptive statistics for alosid meristics (Tables 2, 4 and 6) showed frequent annual variations in the means, modes, and frequency distributions. The direction of change (increase or decrease) in these statistics was not consistent among years or areas, and was not consistent between characters in a given location and year. The lack of consistency in the changes suggests that the meristic characters used in this study are readily modified by environmental fluctuations.

4.3 MULTIVARIATE ANALYSIS

4.3.1. ALEWIFE AND BLUEBACK HERRING

The factorial MANOVA of the meristic characters for river herring indicated that there were significant differences among areas and among years for each species. Additionally, the interaction effects were found to be significantly different (Table 7). The presence of strong statistical evidence for interactions precludes interpretation of significant main effects (Box et al. 1978; Snedecor and Cochran 1980; Hull and Nie 1981; Norusis 1985). Within the realm of MANOVA, we examined the simple effects (areas within years, and years within areas). There was also strong statistical evidence (P's $\leq$ 0.001) that all simple effects were significant (Tables 8 and 9). These findings indicate that the significant interactions (Table 7) were not the result of an unduly large difference between levels of one factor coupled to a modest change between levels of the other factor. The meristic characters used are apparently very plastic. Spacial and spatial temporal differences in meristic frequencies readily occur, with sizable changes in given areas and years producing significant statistical interactions.

4.3.2 AMERICAN SHAD

The MANOVA analyses for American shad (Table 7) indicated a significant difference between years ($P < 0.001$), but the area differences and the area-year interactions were not significant ($P = 0.228$, and $P = 0.466$). These findings were sufficient for us to conclude that the meristic study did not support the premise of river-specific stocks of American shad in the Mattaponi and Pamunkey Rivers. Analysis of the simple effects for areas clearly indicated no significant change in the multivariate spatial arrangement of the meristic characters in either 1978 or 1979 (Table 8). In contrast, the simple effects for years were highly significant in each area (Table 9).

What happens to present analysis if you, as done in past, pool year classes? Do you get separation?

5. DISCUSSION

Reed (1964) examined meristic characters of juvenile blueback herring and concluded that different populations existed in Chesapeake Bay and elsewhere along the eastern coast. His conclusions, however, were subjective evaluations of mean differences and lacked statistical inference. Reed also pooled different year classes, thus confounding any temporal effects.

Nichols (1966) reported significant differences in meristic counts among juvenile American shad collected from the Susquehanna, Rappahannock, York and James Rivers. However, Nichols pooled year classes, and employed multiple F-tests to ascertain differences among rivers.

Based on discriminant function analysis, Fischler (1959) and Hill (1959) defined discrete populations in both The Hudson and Connecticut Rivers. Neither investigation, however, considered the possibility of annual variation in meristic frequencies. Fischler used only one year class, and Hill pooled year classes.

Carscadden and Leggett (1975) examined adult shad from the St. John River, New Brunswick, and concluded that shad home not only to their natal river, but to natal tributaries within that river. Their conclusions were based on a multivariate classification technique (Mahalanobis generalized distance converted to percentage overlap) and univariate multiple t-tests.

Messieh (1977) employed discriminant analysis techniques to examine meristic characters of adult alewives and blueback herring in the St. John River, New Brunswick. He reported significant differences among areas, but concluded that considerable straying occurred in the return of alewives to their natal streams. Messieh also pooled age classes and employed multiple t-tests.

The contrariness of our conclusions, relative to the other findings discussed, is primarily due to differences in methodologies. In meristic and morphometric studies discriminant analysis is frequently used as a classification technique to agglutinate or partition recognizable groups (samples) into discrete populations. The technique may suggest hypotheses, but it does not accommodate the testing of hypotheses. Subsequent support of stock discernment is generally sought through the use of univariate statistics, often multiple F and multiple t-tests. Actually, the rejection of the null hypothesis in MANOVA that group population centroids are equal is a necessary condition for a valid discriminant analysis (Pimentel 1979). In the present study, we arrived at our conclusions through tests of multivariate hypotheses, testing main effects, interactions, and simple effects. The MANOVA model avoided both the subjectivity associated with classification techniques, and the highly questionable propriety of multiple F and multiple t-tests. The application of the MANOVA model herein also demonstrated the need for temporal, as well as spatial, considerations in meristic studies.

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Fig. 1. **Sampling locations of juvenile *Alosa* sp. from Chesapeake Bay.**

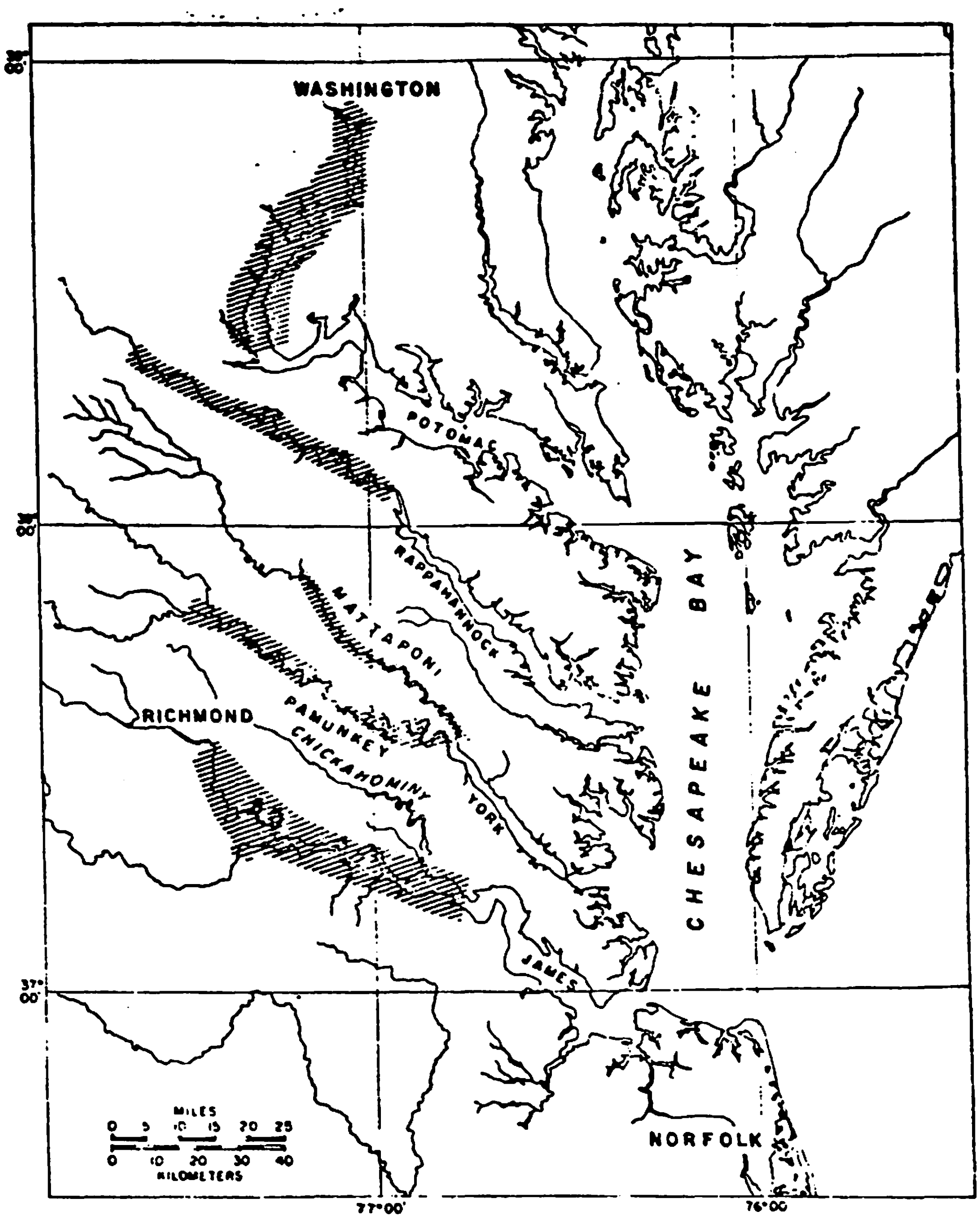

Table 1. Areas sampled, date of capture and size range (mm) of alewives analyzed.

RIVER	DATE OF CAPTURE	SIZE RANGE	N
Potomac	Aug 8, 1978	67-83	50
"	Jul 18, 1979	57-76	50
"	Aug 5, 1980	57-86	50
Rappahannock	Aug 28, 1978	53-75	50
"	Aug 1, 1979	61-73	50
"	Jul 10, 1980	49-61	50
Mattaponi	Oct 5, 1978	57-64	50
"	Jul 14, 1980	65-77	33
Pamunkey	Sep 7, 1978	57-65	50
"	Jul 31, 1979	62-74	50
"	Jul 7, 1980	48-77	38
James	Sep 25, 1978	48-67	50

Table 2. Frequency distributions, means and standard deviations of meristic characters examined for alewife.

RIVER	YEAR	NO. OF DORSAL RAYS 16	17	18	19	N	MEAN	STD. DEV.
Potomac	1978	1	15	33	1	50	17.68	0.5511
"	79	5	28	17		50	17.24	0.6247
"	80	4	35	11		50	17.14	0.5349
Rappahannock	1978	3	21	22	4	50	17.54	0.7329
"	79	2	22	25	1	50	17.50	0.6145
"	80	15	29	6		50	16.82	0.6289
Mattaponi	1978		24	24	2	50	17.56	0.5771
"	80	2	22	9		33	17.21	0.5453
Pamunkey	1978		14	31	5	50	17.82	0.5956
"	79	2	9	38	1	50	17.76	0.5555
"	80	2	21	15		38	17.34	0.5825
James	1978	6	26	18		50	17.24	0.6565

RIVER	YEAR	NO. OF ANAL RAYS 15	16	17	18	19	20	21	N	MEAN	STD. DEV.
Potomac	1978			10	20	19	1		50	18.22	0.7900
"	79			5	15	21	8	1	50	18.70	0.9313
"	80			10	24	16			50	18.12	0.7183
Rappahannock	1978	1	1	5	20	18	5		50	18.36	0.9455
"	79			13	17	20			50	18.14	0.8084
"	80		1	17	25	6	1		50	17.78	0.7637
Mattaponi	1978			14	23	13			50	17.98	0.7420
"	80			12	16	5			33	17.79	0.6963
Pamunkey	1978			8	27	14	1		50	18.16	0.7095
"	79			7	25	15	3		50	18.28	0.7835
"	80			9	16	13			38	18.11	0.7637
James	1978			12	27	11			50	17.98	0.6848

RIVER	YEAR	NO. OF PECTORAL RAYS 12	13	14	15	16	N	MEAN	STD. DEV.
Potomac	1978			10	35	5	50	14.90	0.5440
"	79			12	30	8	50	14.92	0.6337
"	80		2	35	13		50	14.22	0.5067
Rappahannock	1978			4	35	11	50	15.14	0.5347
"	79			6	38	6	50	15.00	0.4949
"	80		2	19	26	3	50	14.60	0.6701
Mattaponi	1978		1	24	23	2	50	14.52	0.6141
"	80		1	25	7		33	14.18	0.4647
Pamunkey	1978	1	2	23	23	1	50	14.42	0.7023
"	79	1	2	11	32	4	50	14.72	0.7570
"	80		3	27	8		38	14.13	0.5287
James	1978			21	28	1	50	14.60	0.5345

Table 2. (continued)

RIVER	YEAR	NO. OF VENTRAL RAYS 7	8	9	10	N	MEAN	STD. DEV.
Potomac	1978	1	4	45		50	8.88	0.3854
"	79		4	46		50	8.92	0.2740
"	80		2	44	4	50	9.04	0.3476
Rappahannock	1978		1	48	1	50	9.00	0.2020
"	79			48	2	50	9.04	0.1979
"	80			48	2	50	9.04	0.1979
Mattaponi	1978		2	46	2	50	9.00	0.2857
"	80			32	1	33	9.03	0.1741
Pamunkey	1978		1	47	2	50	9.02	0.2466
"	79		1	49		50	8.98	0.1414
"	80		2	36		38	8.95	0.2263
James	1978		2	46	2	50	9.00	0.2857

RIVER	YEAR	NO. OF ANTERIOR SCUTES 17	18	19	20	21	22	N	MEAN	STD. DEV.
Potomac	1978		9	36	5			50	18.92	0.5284
"	79		2	33	13	1	1	50	19.32	0.6833
"	80		10	33	7			50	18.94	0.5859
Rappahannock	1978		10	33	7			50	18.94	0.5859
"	79	1	8	36	5			50	18.90	0.5803
"	80		2	38	10			50	19.16	0.4679
Mattaponi	1978	1	16	30	3			50	18.70	0.6145
"	80		3	24	6			33	19.09	0.5222
Pamunkey	1978	1	9	37	2		1	50	18.88	0.6889
"	79	1	6	37	6			50	18.96	0.5700
"	80		7	26	5			38	18.95	0.5670
James	1978	2	11	34	3			50	18.76	0.6247

RIVER	YEAR	NO. OF POSTERIOR SCUTES 12	13	14	15	16	17	N	MEAN	STD. DEV.
Potomac	1978		3	12	31	4		50	14.72	0.7010
"	79	1	11	25	12	1		50	14.02	0.7951
"	80		3	24	23			50	14.40	0.6061
Rappahannock	1978		1	18	23	8		50	14.76	0.7442
"	79		1	18	27	4		50	14.68	0.6528
"	80		2	20	27	1		50	14.54	0.6131
Mattaponi	1978		1	11	30	8		50	14.90	0.6776
"	80			10	17	5	1	33	14.91	0.7650
Pamunkey	1978		2	19	25	4		50	14.62	0.6966
"	79		1	14	32	3		50	14.74	0.5997
"	80			13	25			38	14.66	0.4808
James	1978		2	24	24			50	14.44	0.5771

Table 2. (continued)

RIVER	YEAR	NO. OF TOTAL SCUTES						N	MEAN	STD. DEV.
		31	32	33	34	35	36			
Potomac	1978	1	5	12	26	5	1	50	33.64	0.9424
"	79	1	9	18	18	3	1	50	33.32	0.9781
"	80		6	22	21	1		50	33.34	0.7174
Rappahannock	1978	1	2	16	23	8		50	33.70	0.8631
"	79	2	2	14	29	3		50	33.58	0.8352
"	80		3	18	20	9		50	33.70	0.8391
Mattaponi	1978		6	14	25	4	1	50	33.60	0.8806
"	80			7	20	5	1	33	34.00	0.7071
Pamunkey	1978	3	2	19	21	3	2	50	33.50	1.0349
"	79		1	19	24	16		50	33.70	0.7071
"	80		3	13	18	4		38	33.61	0.7898
James	1978	2	7	20	21			50	33.20	0.8330

Table 3. Areas sampled, date of capture and size range (mm) of blueback herring analyzed.

RIVER	DATE OF CAPTURE	SIZE RANGE	N
Potomac	Aug 8, 1978	43-56	50
"	Jul 18, 1979	44-62	50
"	Jul 10, 1980	46-55	50
Rappahannock	Aug 28, 1978	42-62	50
"	Aug 1, 1979	45-56	50
"	Aug 12, 1980	44-56	50
Mattaponi	Sep 12, 1978	47-57	50
"	Jul 31, 1979	43-55	50
"	Jul 14, 1980	36-62	50
Pamunkey	Sep 7, 1978	43-61	50
"	Jul 31, 1979	46-57	50
"	Sep 10, 1980	44-60	50
James	Sep 26, 1978	43-53	50
"	Jul 31, 1979	50-59	50
"	Jul 15, 1980	40-56	50

Table 4. Frequency distributions, means and standard deviations of meristic characters examined for blueback herring.

RIVER	YEAR	NO. OF DORSAL RAYS				N	MEAN	STD. DEV.
		15	16	17	18			
Potomac	1978		14	36		50	16.72	0.4536
"	79		14	34	2	50	16.76	0.5175
"	80	2	32	15	1	50	16.30	0.5803
Rappahannock	1978		19	30	1	50	16.64	0.5253
"	79		13	34	3	50	16.80	0.5345
"	80	2	15	29	4	50	16.70	0.6776
Mattaponi	1978		14	36		50	16.72	0.4536
"	79		11	36	3	50	16.84	0.5095
"	80		6	32	12	50	17.12	0.5938
Pamunkey	1978		17	30	3	50	16.72	0.5729
"	79		14	33	3	50	16.78	0.5455
"	80		10	33	7	50	16.94	0.5859
James	1978		16	34		50	16.68	0.4712
"	79		11	36	3	50	16.84	0.5095
"	80		19	28	3	50	16.68	0.5869

RIVER	YEAR	NO. OF ANAL RAYS					N	MEAN	STD. DEV.
		16	17	18	19	20			
Potomac	1978	2	26	20	2		50	17.44	0.6440
"	79	1	15	30	4		50	17.74	0.6328
"	80		10	31	9		50	17.98	0.6224
Rappahannock	1978	1	23	24	2		50	17.54	0.6131
"	79	3	19	26	2		50	17.54	0.6764
"	80	1	23	22	4		50	17.58	0.6728
Mattaponi	1978	4	33	13			50	17.18	0.5602
"	79	4	18	27	1		50	17.50	0.6776
"	80	1	29	14	4	2	50	17.54	0.8381
Pamunkey	1978		17	25	7	1	50	17.84	0.7384
"	79	2	27	17	4		50	17.46	0.7060
"	80	1	25	17	7		50	17.60	0.7559
James	1978	3	26	21			50	17.36	0.5980
"	79		20	24	6		50	17.72	0.6713
"	80	2	15	23	9	1	50	17.84	0.8418

Table 4. (continued)

RIVER	YEAR	NO. OF PECTORAL RAYS 12	13	14	15	16	17	N	MEAN	STD. DEV.
Potomac	1978			2	30	18		50	15.32	0.5511
"	79			3	32	15		50	15.24	0.5555
"	80			2	23	23	2	50	15.50	0.6468
Rappahannock	1978			3	24	23		50	15.40	0.6061
"	79			2	23	25		50	15.46	0.5789
"	80			16	28	6		50	14.80	0.6389
Mattaponi	1978			3	39	8		50	15.10	0.4629
"	79	1		6	36	7		50	14.96	0.6688
"	80			26	21	3		50	14.54	0.6131
Pamunkey	1978			3	19	26	2	50	15.54	0.6764
"	79			2	26	22		50	15.40	0.5714
"	80			29	20	1		50	14.44	0.5406
James	1978			1	33	16		50	15.30	0.5051
"	79			4	27	19		50	15.30	0.6145
"	80			16	30	3	1	50	14.78	0.6481

RIVER	YEAR	NO. OF VENTRAL RAYS 8	9	10	N	MEAN	STD. DEV.
Potomac	1978	2	48		50	8.96	0.1979
"	79		48	2	50	9.04	0.1979
"	80	1	49		50	8.98	0.1414
Rappahannock	1978		49	1	50	9.02	0.1414
"	79	1	46	3	50	9.04	0.2828
"	80		49	1	50	9.02	0.1414
Mattaponi	1978	2	48		50	8.96	0.1979
"	79		50		50	9.00	0.0000
"	80		48	2	50	9.04	0.1979
Pamunkey	1978	1	44	5	50	9.08	0.3405
"	79		49	1	50	9.02	0.1414
"	80		49	1	50	9.02	0.1414
James	1978	1	48	1	50	9.00	0.2020
"	79	1	47	2	50	9.02	0.2466
"	80		49	1	50	9.02	0.1414

Table 4. (continued)

RIVER	YEAR	NO. OF ANTERIOR SCUTES 18	19	20	21	22	N	MEAN	STD. DEV.
Potomac	1978			28	21	1	50	20.46	0.5425
"	79		2	19	29		50	20.54	0.5789
"	80		12	38			50	19.76	0.4314
Rappahannock	1978		1	13	36		50	20.70	0.5051
"	79	1	2	9	37	1	50	20.70	0.6776
"	80		11	35	4		50	19.86	0.5349
Mattaponi	1978			17	33		50	20.66	0.4785
"	79		1	6	43		50	20.84	0.4219
"	80		8	33	9		50	20.02	0.5887
Pamunkey	1978			22	28		50	20.56	0.5014
"	79		1	9	38	2	50	20.82	0.5226
"	80	1	11	38			50	19.74	0.4870
James	1978		2	22	26		50	20.48	0.5799
"	79	1	2	19	26	2	50	20.52	0.7351
"	80		19	29	2		50	19.66	0.5573

RIVER	YEAR	NO. OF POSTERIOR SCUTES 12	13	14	15	16	17	N	MEAN	STD. DEV.
Potomac	1978		15	27	8			50	13.86	0.6704
"	79		12	34	4			50	13.84	0.5481
"	80			9	37	4		50	14.90	0.5051
Rappahannock	1978		2	30	18			50	14.32	0.5511
"	79	1	10	27	11	1		50	14.02	0.7690
"	80			10	27	13		50	15.06	0.6824
Mattaponi	1978		4	31	15			50	14.22	0.5817
"	79		2	26	22			50	14.40	0.5714
"	80		1	4	31	14		50	15.16	0.6503
Pamunkey	1978		7	27	14	2		50	14.22	0.7365
"	79	3	13	28	6			50	13.74	0.7508
"	80		1	13	24	12		50	14.94	0.7669
James	1978		2	29	19			50	14.34	0.5573
"	79		5	33	11	1		50	14.16	0.6181
"	80		1	5	26	17	1	50	15.24	0.7440

Table 4. (continued)

RIVER	YEAR	NO. OF TOTAL SCUTES							N	MEAN	STD. DEV.
		31	32	33	34	35	36	37			
Potomac	1978			8	20	20	2		50	34.32	0.7939
"	79		2	5	17	23	3		50	34.40	0.9035
"	80			3	14	30	3		50	34.66	0.6884
Rappahannock	1978			1	8	30	11		50	35.02	0.6848
"	79	2		2	12	24	10		50	34.72	1.0887
"	80			2	14	21	12	1	50	34.92	0.8769
Mattaponi	1978			2	11	28	9		50	34.88	0.7461
"	79			1	5	25	19		50	35.24	0.7160
"	80			2	5	26	16	1	50	35.18	0.8003
Pamunkey	1978			5	12	23	9	1	50	34.78	0.9322
"	79		2	4	13	26	5		50	34.56	0.9293
"	80			5	16	19	10		50	34.68	0.9134
James	1978		1		13	29	7		50	34.82	0.7475
"	79		1	3	17	20	8	1	50	34.68	0.9570
"	80		1	1	15	20	11	2	50	34.90	0.9742

Table 5. Areas sampled, date of capture and size range (mm) of American shad analyzed.

RIVER	DATE OF CAPTURE	SIZE RANGE	N
Mattaponi	Sep 12, 1978	53-62	50
"	Jul 31, 1979	47-66	50
Pamunkey	Sep 7, 1978	45-69	50
"	Aug 21, 1979	50-72	50
"	Jul 7, 1980	43-64	50
James	Sep 25, 1978	86-104	50

Table 6. Frequency distributions, means and standard deviations of meristic characters examined for American shad.

RIVER	YEAR	NO. OF DORSAL RAYS 15	16	17	18	19	N	MEAN	STD. DEV.
Mattaponi	1978		3	24	22	1	50	17.42	0.6417
"	79		3	28	17	2	50	17.36	0.6627
Pamunkey	1978		6	33	11		50	17.10	0.5803
"	79	1	3	26	20		50	17.30	0.5928
"	80		1	10	32	7	50	17.90	0.6465
James	1978		6	30	14		50	17.16	0.6181

RIVER	YEAR	NO. OF ANAL RAYS 17	18	19	20	21	22	N	MEAN	STD. DEV.
Mattaponi	1978			14	24	11	1	50	19.98	0.7690
"	79			8	30	11	1	50	20.10	0.6776
Pamunkey	1978		2	15	23	8	2	50	19.86	0.8809
"	79	1	1	7	24	15	2	50	20.14	0.8081
"	80			3	22	20	5	50	20.54	0.7624
James	1978		4	25	15	6		50	19.46	0.8134

RIVER	YEAR	NO. OF PECTORAL RAYS 15	16	17	18	19	20	N	MEAN	STD. DEV.
Mattaponi	1978	2	32	15	1			50	16.30	0.5803
"	79	4	22	24				50	16.40	0.6389
Pamunkey	1978	5	36	9				50	16.08	0.5284
"	79	3	21	25			1	50	16.52	0.6131
"	80	19	30	1				50	15.64	0.5249
James	1978	14	35	1				50	15.74	0.4870

RIVER	YEAR	NO. OF VENTRAL RAYS 8	9	10	N	MEAN	STD. DEV.
Mattaponi	1978	3	47		50	8.94	0.2399
"	79	1	48	1	50	9.00	0.2020
Pamunkey	1978	4	46		50	8.92	0.2740
"	79	2	47	1	50	8.98	0.2470
"	80	3	46	1	50	8.96	0.2834
James	1978	12	38		50	8.76	0.4314

Table 6. (continued)

RIVER	YEAR	NO. OF ANTERIOR SCUTES 18	19	20	21	22	23	N	MEAN	STD. DEV.
Mattaponi	1978		3	20	23	4		50	20.56	0.7329
"	79		1	23	18	8		50	20.66	0.7722
Pamunkey	1978		1	21	24	4		50	20.62	0.6667
"	79		2	20	16	12		50	20.76	0.8992
"	80		3	16	22	8	1	50	20.76	0.8699
James	1978	3	1	26	18	2		50	20.30	0.8391

RIVER	YEAR	NO. OF POSTERIOR SCUTES 14	15	16	17	18	N	MEAN	STD. DEV.
Mattaponi	1978			26	23	1	50	16.50	0.5440
"	79	1	18	22	9		50	15.78	0.7637
Pamunkey	1978	2	6	21	21		50	16.22	0.8154
"	79		25	21	4		50	15.58	0.6667
"	80		13	28	9		50	15.92	0.6645
James	1978		5	21	21	3	50	16.44	0.7602

RIVER	YEAR	NO. OF TOTAL SCUTES 34	35	36	37	38	39	N	MEAN	STD. DEV.
Mattaponi	1978		2	11	23	10	4	50	37.06	0.9564
"	79		8	21	13	7	1	50	36.44	0.9930
Pamunkey	1978	1	4	10	22	13		50	36.84	0.9765
"	79	2	11	14	16	5	2	50	36.34	1.1911
"	80	1	7	14	15	11	2	50	36.68	1.1513
James	1978	1	4	14	21	8	2	50	36.74	1.0264

Table 7. Summary of the factorial multivariate analysis of variance of alewife, blueback herring and American shad meristic characteristics.

Factor or interaction	Species	Wilks criterion	Approx. F value	Probability
Areas	Alewife	0.755	8.31	<0.001
	Blueback	0.795	6.18	<0.001
	Shad	0.959	1.37	0.228
Years	Alewife	0.724	14.77	<0.001
	Blueback	0.444	52.14	<0.001
	Shad	0.752	10.56	<0.001
Areas-Years	Alewife	0.846	2.88	<0.001
	Blueback	0.767	3.55	<0.001
	Shad	0.971	0.94	0.466

Table 8. Summary of the multivariate analysis of the simple effects of areas within years for alewife, blueback herring, and American shad.

Species	Year	Wilks' Criterion	Approximate F value	Probability
Alewife	1978	0.865	4.168	<.001
	1979	0.853	6.949	<.001
	1980	0.890	3.341	<.001
Blueback herring	1978	0.902	3.195	<.001
	1979	0.897	3.360	<.001
	1980	0.769	8.321	<.001
American shad	1978	0.943	1.921	0.079
	1979	0.988	0.394	0.883

Table 9. Summary of the multivariate analysis of the simple effects of years within areas for alewife, blueback herring, and American shad.

Species	Area	Wilks' Criterion	Approximate F value	Probability
Alewife	Potomac	0.791	10.446	<.001
	Rappahannock	0.857	6.741	<.001
	Mattaponi	0.954	4.082	<.001
	Pamunkey	0.926	3.285	<.001
Blueback herring	Potomac	0.758	18.091	<.001
	Rappahannock	0.797	14.632	<.001
	Mattaponi	0.811	13.452	<.001
	Pamunkey	0.703	23.429	<.001
	James	0.774	16.623	<.001
American shad	Mattaponi	0.863	5.054	<.001
	Pamunkey	0.832	6.453	<.001