Aspects of the Life History of the Atlantic Silverside (*Menidia Menidia*) of the Annapolis River, Nova Scotia

B. M. Jessop

Freshwater and Anadromous Division
Fisheries Research Branch
Department of Fisheries and Oceans
Halifax, Nova Scotia, B3J 2S7

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ASPECTS OF THE LIFE HISTORY OF THE ATLANTIC SILVERSIDE (*MENIDIA MENIDIA*) OF THE ANNAPOLIS RIVER, NOVA SCOTIA

B.M. Jessop

Freshwater and Anadromous Division
Fisheries Research Branch
Department of Fisheries and Oceans
Halifax, Nova Scotia
B3J 2S7

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Aspects of the life history of the Atlantic silverside, *Menidia menidia*, including seasonal distribution, age structure, sex ratio, growth rate, maturation and fecundity, were studied in the stratified, tidally restricted estuary of the Annapolis River, Nova Scotia. Adult silversides migrated into the estuary in April and May, spawned mainly in June and returned to sea between July and October. During spawning, adults were most abundant in the middle reaches of the estuary.

Annapolis River silversides, which are near the northern limit of their range, have a greater proportion of Age-2 fish than do more southern populations. In all age groups, females are about twice as abundant as males. As a consequence of the shorter northern growing season, juveniles average smaller than do more southern populations, in spite of their faster growth rate. Maximum adult lengths are similar throughout the species range, but southern fish are Age 1 while northern fish reach Age 2. Females grew faster and lived longer than males, thereby attaining larger maximum sizes. Estimates of the von Bertalanffy growth-function parameters L_∞, K and t_0 for males were, 122.2 mm, 1.00 and -0.348; and for females, 128.2 mm, 1.04 and -0.305. A seasonal growth curve was more realistic and fitted the data better. The instantaneous rate of natural mortality (M) was similar (1.3) for both sexes.

Sexual maturation and spawning first occur at Age 1. Fecundity increased with fish length, weight and age, ranging from about 700 to 3,100 ova/female. Age-2 females make an important contribution to population fertility.

Insights into the life history of Atlantic silversides and the consequences for fishery management can be gained by viewing the species in terms of r- and K-selection theory. Silversides are typical r-strategists.

Key words: Atlantic silverside (*Menidia menidia*), life-history, Maritime Provinces, Annapolis River, abundance, maturation, growth rate, size, age, sex, fecundity, distribution.

RÉSUMÉ

Jessop, B.M. 1983. Aspects of the life history of the Atlantic silverside (*Menidia menidia*) of the Annapolis River, Nova Scotia. Can. MS Rep. Fish. Aquat. Sci. No. 1694. ix + 41 p.

On a étudié les divers aspects du cycle biologique de la capucette, *Menidia menidia*, y compris la distribution saisonnière, la structure par âge, la proportion des sexes, la croissance, la maturation et la fécondité, dans l'estuaire de la rivière Annapolis (Nouvelle-Ecosse), estuaire stratifié, où le jeu des marées est entravé. Les capucettes pénètrent dans l'estuaire en avril et mai, pondent principalement en juin et retournent à la mer entre juillet et octobre. Durant la ponte, les adultes sont le plus abondants dans l'estuaire moyen.

Parmi les capucettes de la rivière Annapolis, qui se trouve près de la limite septentrionale de l'aire de l'espèce, la proportion des poissons d'âge 2 est plus forte que chez les populations méridionales. Dans tous les groupes d'âge, il y a environ deux fois plus de femelles que de mâles. Parce que la saison de croissance est plus courte au nord, les jeunes sont en moyenne plus petits qu'au sud, en dépit d'un taux de croissance plus rapide. La longueur maximale des adultes est la même dans toute l'aire, mais les poissons du sud l'atteignent à l'âge 1 tandis que ceux du nord à l'âge 2. Les femelles croissent plus rapidement et vivent plus longtemps que les mâles, de sorte qu'elles atteignent des longueurs maximales plus grandes. Des estimations des paramètres de croissance de von Bertalanffy L_∞, K et t_0 sont de 122,2 mm, 1,00 et -0,348 pour les mâles; et 128,2 mm, 1,04 et -0,305 pour les femelles. Une courbe de croissance saisonnière est plus réaliste et s'adapte mieux aux données. Le taux instantané de mortalité naturelle (M) est identique (1,3) chez les deux sexes.

La maturation sexuelle et la ponte se produisent pour la première fois à l'âge 1. La fécondité augmente en fonction de la longueur, du poids et de l'âge des sujets, variant d'environ 700 à 3 100 oeufs par femelle. Les femelles d'âge 2 contribuent de façon significative à la fécondité de la population.

On comprend mieux le cycle biologique des capucettes et ses conséquences pour la gestion des pêches quand on étudie l'espèce à la lumière de la théorie de sélection r et K. Les capucettes sont des "stratégistes r" typiques.

INTRODUCTION

The Atlantic silverside (*Menidia menidia*) is the sole representative of the family Atherinidae occurring in Atlantic Canada. It is widely distributed in the estuaries and inshore waters of the Maritimes, from the Miramichi River estuary of New Brunswick, through Prince Edward Island and Nova Scotia, in the southern Gulf of St. Lawrence to the Bay of Fundy, although it is less frequently found along the Atlantic Coast of Nova Scotia (Leim and Scott 1966). In Prince Edward Island, its abundance is sufficient to support a moderate commercial fishery (1979 catch 276 t; Jessop and Morantz 1982), presently the only one in the Maritimes. In the Annapolis River, silversides are abundant in that portion of the estuary upstream of the causeway at Annapolis Royal (Jessop 1976; Daborn et al. 1979).

This study was prompted by the scarcity of information on the life history of the silverside in the Maritimes, given its developing importance as a commercial resource and its probable importance as forage for the striped bass (*Morone saxatilis*), which supports a popular sport fishery in the Annapolis River (Jessop 1980). Its objectives were to establish the distributional and seasonal differences in the abundance and growth of silversides within the Annapolis River; to determine the relations between age, sex and fish size; and to examine aspects of the fecundity, reproduction and life history of the species.

DESCRIPTION OF THE STUDY AREA

The Annapolis River flows southwestward for about 142 km to empty into the Annapolis Basin in southwestern Nova Scotia (Fig. 1). Digby Gut connects the basin to the Bay of Fundy. The river meanders extensively along the gently sloping valley floor, which decreases about 40 m in elevation between source and tidewater.

A causeway at Annapolis Royal normally limits upstream tidal fluctuations to about ±0.5 m (Jessop 1976) but permits free passage of fish through a permanently open 3-m x 7-m fishway. Downstream of the causeway, the tidal amplitude ranges from 7 m to 9 m. The head of tide is located about midway between Bridgetown and Paradise (approximately km 34).

The headpond is approximately 4.1 km long and 0.7 km-1.6 km wide. A maximum depth of 21 m occurs about 1 km upstream of the causeway but much of the headpond is 9 m deep. Depths diminish with upstream progression from 12 m at the first narrows (km 4) to 6 m at km 9, to 3 m between km 19 and km 30 (Bridgetown) and are generally 2 m above km 30.

The river upstream of the causeway is an extensive, highly stratified estuary, with a wedge of saline water overlain by outflowing low-salinity water. Salinities at various depths and locations vary seasonally according to weather conditions, river discharge pattern, tidal flow and manipulation of headpond and river levels (Daborn et al. 1979). Surface salinities beyond 16 km upriver of the causeway are less than 5‰. Salinities in the salt wedge typically exceed 20‰.

Near the causeway, pH values fluctuate around neutrality at all depths; but upstream, the surface water becomes increasingly acidic, until near km 30 where the pH at all depths varies little (6.2-6.6) during the summer. Daborn et al. (1979) conclude that the river is "chemically unexceptional" except for rather high levels of inorganic phosphorus and nitrate, which probably contribute to the productivity of the estuary.

Additional descriptive details may be found in Jessop (1976), and Daborn et al. (1979; 1979a).

METHODS

BIOLOGICAL SAMPLING

Between June 4 (late June for Site 1) and September 29, 1980, regular seine collections were made at five sites between the Annapolis Causeway (km 0) and a point (km 22) near Tupperville (Fig. 1). The first four sites were spaced at intervals of 3 km-5 km and the fifth 9 km upriver. Weekly seinings were made until mid-July, then biweekly until early September, with a final collection in late September. Site selection was based on previous surveys by Jessop (1976), Williams (1978) and Daborn et al. (1979a), which describe the distribution of silversides in the river and the location of shelving beaches and shallow ledges suitable for seining.

A 15.2-m x 2.4-m bag seine, with mesh sizes of 13 mm in the wings and 6 mm in the bag, was used for all sampling. Repeated seine hauls, to a maximum of six at each site, were employed as necessary to obtain samples of up to 70 specimens each of adult and juvenile silversides. Captured silversides were counted and released except for the required sample.

Sampled silversides were measured for fork and total length (to nearest mm) and, following blotting, weighed (to nearest 0.01 g). Total lengths were recorded for juveniles with an undeveloped caudal fin fork. Fork lengths are employed throughout this report unless otherwise noted. Sex and state of maturity, based upon criteria given by Nikolsky (1963), were determined by visual examination of the gonads of all adult fish (except during the first week, when maturity was recorded only for fish that were scale sampled) and most juveniles exceeding 65 mm (below 65 mm, sex was not readily confirmed without the use of a microscope). The criteria used to visually distinguish the gonads of immature unripe fish of each sex (testes were thread-like and translucent or opaque, while ovaries were more sausage-like and enclosed by a greyish-black membrane) were similar to those used by Snelson and Wetherington (1980) for a similarly sized poeciliid and were confirmed histologically (Jessop and Morantz 1982).

A scale sample was collected for every second adult fish and for almost all fish exceeding 100 mm. Scale samples were not normally taken from juvenile fish, since they were readily distinguished by their relative size. Scales were collected from three sites in late September.

Daily water temperatures were taken at Bridgetown at 1 m depth with a recording thermograph. Although surface-water temperatures taken at the sampling sites averaged 2.5°C higher (range 1.3°-2.9°C), the Bridgetown temperatures may be used as an index of the minimum daily temperatures in the sampling areas because water temperatures are essentially uniform between the surface and 2 m depth (Daborn et al. 1979a).

Scales were independently aged twice under 20x magnification. Where differences occurred, a third examination was made and majority agreement accepted as the correct age. It quickly became apparent that annulus formation occurred following spawning; thus a virtual annulus was assumed at the scale margin when appropriate.

For adult silversides from which no scale samples were taken, ages were assigned on the basis of their length and date of capture, since division according to age and sex of fish aged by scales showed virtually no overlap between groups; i.e., male, Age-1 fish were smaller than male, Age-2 fish. For each sex-group for a given sample date, a non-scale-sampled fish was assigned Age 1 if its length was less than the maximum length of Age-1 scale-sampled fish or if its length was 3 mm or more less than the minimum length of Age-2 fish (over 98% of fish assigned Age 1 were more than 5 mm smaller and most were more than 10 mm smaller). Age 2 was assigned those fish that exceeded the minimum length of Age-2 scale-sampled fish from a given sample date. Where an age-sex category for a given date contained no aged fish, the length-range values for the sample period immediately preceding were used. In only one sample was there a length overlap between ages (Appendix A). This required the elimination of four fish which could not definitely be assigned an age. The distribution of aged and assigned-age fish is presented in Appendix B.

Ovaries were excised from a representative series of fish of all maturity stages, including those used for fecundity analysis, and weighed to the nearest 0.1 g. The maturity index was defined as the total ovary weight divided by the total body weight (Vladykov 1956). Condition was calaculated as:

$$k = \frac{\text{total weight - gonad weight (g)} \times 100}{\text{fork length}^3\ \text{(cm)}}$$

Subtraction of the gonad weight permits comparison of somatic condition between seasons without the confounding effects of gonad maturation (Ricker 1975). Up to 16 ovary samples per 5-mm increment over the size range of ripe females (Maturity Stages 4 and 5) were preserved in Gilsons fluid. Care was taken to ensure that eggs had not been shed during the process of sample collection. During washing and cleaning, the eggs were flushed gently through a sieve with a 0.5-mm mesh to separate the maturing and ripe ova (the larger, somewhat translucent yellow or yellow-orange ova) from the immature "recruitment stock" and atretic ova (smaller, opaque, often whitish ova - hereafter termed non-mature ova) which were retained on a 0.2-mm mesh sieve. Trials with several mesh sizes established that the 0.5-mm mesh was most suitable for preliminary sorting of the eggs into large and small size-groups and that virtually nothing but the ovarian tissue debris passed the 0.2-mm mesh. Both portions were then air dried following Simpson's dry method (Bagenal and Braum 1978) and weighed to the nearest 0.1 mg.

Dried ova diameters (one axis) were measured with an ocular micrometer (±0.05 mm) for six samples of 40 ova each, randomly chosen from the ova fractions > 0.5 mm and < 0.5 mm. About 21% of the ova (range 0%-42%) of the < 0.5-mm fraction were non-mature and were not removed by the filtering process, but these were readily segregated in the counting process by virtue of their small size and later added to the < 0.5-mm fraction. All mature ova in each sample were manually and individually counted with the aid of a binocular microscope. Numbers of non-mature ova were estimated by counting their number in four samples (mean maturity index 23.3), by determining the mean weight/100 ova, then by dividing the weights of the non-mature fraction by this factor. Counts of mature ova were added to estimates of non-mature ova for each sample to obtain absolute fecundity (Bagenal 1978).

STATISTICAL METHODS

The adult (Ages 1 and 2) length data for each sampling site were sub-divided according to age-sex group, i.e., male Age 1, female Age 1, male Age 2 and female Age 2. For each site, one-way analyses of covariance (ANCOVA) were used to test for differences in length (Y) according to sex, age and date of collection (X). Linear contrasts were used to compare age and sex groupings.

Differences in juvenile (Age 0) lengths according to date of collection were examined for each site by one-way analyses of variance with the "among dates sum of squares" divided into that due to regression over time and that due to unexplained variability. A logarithmic (base 10) transformation of the independent variable (date) was used to linearize the regression line. Although second-degree polynominal regressions provided significantly better fits to the juvenile data than did linear regressions, the improvement in fit according to the r^2 values (coefficients of determination) was less than 2% in all cases except Site 1, where it was 19%. Accordingly, the simpler linear regression has been presented, since the conclusions for both analyses are identical.

Tests were made for violations of certain of the assumptions implicit in the use of the analysis of variance (Snedecor and Cochran 1980). The assumption that the residuals (observed minus predicted values) are normally distributed with constant variance was tested by examination of plots of standardized residuals versus the independent variable (Draper and Smith 1966). Normality of the sample data was examined by calculating the Kolmogorov-Smirnov D statistic while Levene's test was employed to check for homogeneity of variances (Snedecor and Cochran 1980). The independence of residuals was assumed, based on the manner in which the samples were collected.

Statistical packages used for analysis of the data included those for the Hewlett-Packard HP-45 and the BMDP1V program package (BMDP-79 1979).

The generalized (4-parameter) von Bertalanffy growth function (VBGF) was fitted to mean length-at-age data, weighted by sample size, according to the procedure described by Gaschutz et al. (1980) for fitting seasonally oscillating length data. Mean lengths-at-age (using fractional monthly intervals) were obtained by combining the data for all sites during a given sampling period. The standard, 3-parameter version of the VBGF was also fitted for comparison and to obtain parameter estimates suitable for estimating M, the instantaneous rate of natural mortality, as described by Pauly (1980).

The geometric-mean regression model (Ricker 1973) was used in calculating length:weight, fork-length:total-length and fecundity:length relationships. Up to 30 length:weight pairs per 10-mm length interval were randomly chosen from the data set collected after the end of the spawning season. The fork-length: total-length relationship was based on fifteen data pairs per 5-mm fork-length interval between 20 mm and 130 mm, randomly chosen from the entire data set. Prior to measurable (1-mm) separation between fork and total lengths, only total lengths were used. The final two intervals contained ten and six data pairs, respectively.

RESULTS

ABUNDANCE AND DISTRIBUTION

The relative abundance of adult and juvenile Atlantic silversides, as indicated by catch per seine haul, varied between sampling sites and between collection dates at each site during the period from early June to late September. Abundance, as indicated by catch-per-unit-effort, was greatest in the lower and middle reaches of the estuary (Fig. 2 and Appendix C). As the summer progressed, the pattern and magnitude of adult abundance shifted such that, between early June and mid-July, adults declined from abundance to scarcity or absence at the two sites furthest upstream (Site 5 at km 22 and Site 4 at km 13), while increasing synchronously at the middle and lower sites (Site 3 at km 8 and Site 2 at km 3) before declining abruptly in early August. At the causeway (Site 1, km 0), the usually low adult densities peaked sharply in early August. By late September, adults were absent at all but one site located in the lower estuary.

Young-of-the-year were first captured at all sites in early July. Prior to mid-July, young silversides were too small to be sampled efficiently by the seine that was used. Juvenile abundance was lowest at Site 5, the furthest upstream, throughout the sampling period and was greatest at the middle sites, except during September when abundance was greatest at the causeway. Catch-per-unit-effort declined between early August and late September at all sites except Site 1, where it remained relatively constant.

ANNULUS FORMATION

Annular marks representing spawning checks were deposited on silverside scales between mid-June and late July (Fig. 3). Comparison of gonad maturity state with the presence or absence of an annulus indicates that with few exceptions fish in Maturation Stages 3 through 5, i.e., prior to spawning, did not possess a check; while those in Maturation Stages 6 and 2, i.e., post spawning, did. Scales from juvenile fish collected in late October were similar in appearance to those of yearlings obtained in early June. The scale check laid down following spawning was typical of those deposited during periods of slow growth, having narrowly spaced circuli and crossing over (Bagenal and Tesch 1978).

AGE AND GROWTH

Of the 1,364 adult silversides assigned ages, 6.1% were two years old and 93.9% were one year old. Adult (Age-1 and -2) silversides averaged about 90 mm long and weighed 5.8 g in early June; but by early August, lengths and weights exceeded 100 mm and 7.7 g, respectively (Appendix D). Age-1 silversides, which averaged about 87 mm in early June, typically exceeded 110 mm by late September, a gain of over 20 mm (Appendix E). Corresponding weights increased from about 5.5 g to over 10 g. Age-2 silversides grew more slowly, from 110 mm or more in June to over 120 mm by September (Appendix F). Juvenile (Age-0) silversides grew rapidly from less than 30 mm and 0.15 g in early July to more than 70 mm and 2 g by late September (Appendix G).

Plots of standardized residuals versus the independent variable (date) of the adult data for each site indicated slight heterogeneity of the variances of the sampled lengths as well as slight non-normality of distribution. Much of this resulted from the presence of two age-groups with different mean lengths and little overlap, such that the presence of greater numbers of Age-2 fish in a sample resulted in a higher variance and a longer-tailed, more skewed distribution. Separation by age resulted in homegeneity of most sample variance ($P > 0.05$ for Age 1 and 2 at all except Site 3, where $P = 0.01$ for Age 1, according to Levene's test) and normal sample distributions.

For juvenile silversides, heterogeneity of sample length of variance was highly significant ($P < 0.001$ at all sites). The often skewed, sometimes bimodal, distributions of the juvenile samples probably account for much of the heterogeneity of variances (Fig. 4). Although a rough linear relation between the means and standard deviations was evident for two sites, it was concluded that logarithmic transformation of the length data was unnecessary, since no conclusions in subsequent ANOVA's were changed by its use and it did little to reduce the heterogeneity of variances except in two of five cases. In these two cases, much of the heterogeneity could be attributed to one or two samples with atypical variances. Use of Satterthwaite's rule (Snedecor and Cochran 1980), with both adult and juvenile data, resulted in minor reductions in the denominator degrees of freedom of the F-tests but changed no conclusions as to significance or non-significance.

Fortunately, most parametric statistical analyses tend to be very robust in response to violations of assumptions if they are based on a large number of error degrees of freedom (Harris 1975), a condition that is met here in almost all cases. The consequences of moderate non-normality of error and heterogeneity of variances, as in the adult data, are not serious for overall F-tests as used in analyses of variance. Even the more marked non-normality and heterogeneity of the juvenile data fit within the guidelines given by Harris (1975), within which two-tailed F-tests are generally valid, even on extremely normal populations.

Linear contrasts between the lengths of adult silversides grouped by age and sex indicated that silversides were significantly ($P < 0.001$) smaller at Age 1 than at Age 2 and that males were smaller than females (Table 2). The significant ($P < 0.001$) interaction term supports division into age-sex groups.

Covariance analysis of the lengths of adult silversides, using date as the covariate, revealed significant ($P < 0.05$) differences between the regression slopes of Age-1 males and females and Age-2 females from different sites (Table 2). The regression slopes for male and female Age-1 fish and female Age-2 fish were significantly ($P < 0.05$) steeper at the downriver sites (2 and 3) than at the upriver sites (4 and 5)(Tables 3 and 4). Female Age-2 silversides from Site 3 were unique in having a non-significant ($P > 0.05$) negative rather than positive slope, most likely a consequence of sampling variability. Male Age-2 silversides can be considered to have a common slope not significantly different from zero ($P < 0.05$). Sampling data explained from less than 1% to more than 53% of the total variance (r^2) in length of age-sex groups from different sites. Within each age-sex group, the combination of significant differences between sites in regression slopes and mean lengths resulted in a changing pattern of relationships. In early June, large fish of both ages and sexes tended to be found further upstream (Table 5 and Fig. 5). By July 1 the differences in length between sites were minimized, while by mid-July they were again widening. In summary, the smaller silversides found at the downriver sites grew faster than the initially larger fish at the upriver sites, such that by mid-July they equalled or exceeded the length of the latter groups. This pattern was more evident in Age-1 than in Age-2 fish because of their more rapid seasonal growth. Age-2 males apparently grew little at any site during this time period.

An overview of adult silverside growth dynamics within the Annapolis River estuary was obtained by combining, from all sites, the lengths of each age-sex group. Significant differences ($P < 0.001$) occurred in growth rate between age-sex groups (Table 6). The regression of length with time accounted for from 8% to 41% of the total variance within an age-sex group (Table 3). Regression slopes were significant ($P < 0.05$) for Age-1 males and females and Age-2 females (but marginally so). Age-1 females grew more rapidly; i.e., had a steeper slope than did other age-sex groups, which did not differ significantly ($P > 0.05$) between themselves (Table 7). Between June 1 and July 15, Age-1 silversides remained smaller than Age-2 fish and males of each age-group remained smaller than females. The observed lengths for each age-sex group (all sites combined) are graphed (Fig. 6).

The mean lengths of junveile (Age-0) silversides differed significantly ($P < 0.001$) between sample dates at all sites, with much of the difference accounted for by growth in length over time (Table 8). Differences in mean lengths between sampling dates and heterogeneous sample variances likely account for much of the significance of the residual variances (deviations from regression). In addition, the sample distributions were often far from normal, some being bimodal (Fig. 4). By late September, the samples were typically unimodal. Rates of growth, as indicated by the regression slopes, differed significantly ($P < 0.001$) between sites, being greatest at Site 2, least at Site 1 and intermediate and similar at Sites 3, 4 and 5 (Tables 8 and 9). In comparing regression lines, the assumption of homogeneous variances about the regressions was not met ($F_{[344,379]} = 1.81$, $P < 0.001$). Exclusion of Site 1 did not alter either above conclusion.

Male and female silversides (juvenile and post-spawning fish) did not differ significantly in their length-weight relationship (equality of slopes $F_{[1,352]} = 0.027$, $P = 0.87$; equality of adjusted means $F_{[1,353]} = 0.027$; $P = 0.87$). The length-weight regression equation (sexes combined) was: $Y = -5.2208 + 3.0231X$, where Y = log weight (g), X = log length (mm) and $n = 338$, $r^2 = 0.995$, $s^2_{Y \cdot X} = 0.0030$. The 95% confidence interval about the slope was $V \pm 0.0228$. Confidence intervals (95%) about an estimated weight ($\hat{Y}$) at lengths from 20 mm to 120 mm at 20-mm intervals ranged from log $Y \pm 0.1079$ at 20 mm to log $Y \pm 0.1077$ at 60 mm with log Y $\pm$ 0.1078 at all other lengths.

Conversions between fork length and total length can be made from the relationship: $Y = 0.8106 + 0.9345X$, where Y = fork length (mm) and X = total length (mm), with $n = 316$, $r^2 = 0.9996$. The 95% confidence limit for the regression coefficient was $V \pm 0.0021$, and for an estimated fork length ($\hat{Y}$) was less than $Y \pm 0.14$ mm over the range of total lengths from 20 mm to 120 mm.

Growth rates declined with increasing age, with differential growth rates between sexes becoming distinguishable at lengths of 45 mm-55 mm (Fig. 7). Predicted asymptotic lengths derived from the von Bertalanffy growth function (VBGF) were longer for females than for males, whether seasonal growth was assumed or not (Table 10). The values of the ratios L_{max}/L_∞ were similar for both males and females (1.00 and 0.99, respectively), where L_{max} is the maximum observed length reached in nature for the population considered and L_∞ is the asymptotic length calculated from the 3-parameter VBGF. The ratio L_m/L_∞ was also similar for each sex (about 0.70), where L_m is the length at first reaching maturity. The 4-parameter VBGF fit the data better (had a higher r^2 value) than did the 3-parameter form, while the incorporation of seasonal growth fit best of all.

The generalized or 4-parameter VBGF can, according to Pauly (1981), be written $L_t = L_\infty (1 - e^{-KD(t-t_o)})^{1/D}$, where L_t is the length of an individual at time t, L_∞ is asymptotic size, K and t_o are growth parameters and D is a surface-factor parameter. When D = 1.0, the generalized VBGF reduces to the normal 3-parameter form where $L_t = L_\infty (1 - e^{-K(t-t_o)})$. To account for seasonal growth, an additional constant (C) is introduced as well as the parameter T_s, which expresses the time between birth (at t = o) and the start of the first growth oscillation that is, in this formulation, modulated by a sine-wave curve with a one-year period (Gaschütz et al. 1980).

The plot of the 3-parameter seasonal growth curve shows an "overshoot-undershoot" phenomenon during the winter no-growth period. This phenomenon is a consequence of the use of a sine function in fitting the seasonal growth curve, given the wide range of Y values, the high growth rate of the species and the absence of data points during the winter period. A more complex, periodic function, which could create difficulty in equation solution, would be required to more closely fit the data. A smooth line between growth cessation in autumn and resumption in spring more realistically approximates the discontinuous growth that occurs during a year. The growing season was probably extended from late April-early May to late October-early November, during which period water temperatures can be expected to exceed 6°-8°C (Envir. Canada 1976) and feeding would occur (Conover and Ross 1982), and has arbitrarily been set from May 1 to October 30. According to the seasonal, 3-parameter VBGF curve, male and female juvenile silversides grew approximately 0.70 mm/day (21 mm/month) and 0.74 mm/day (23 mm/month), respectively, between June 15, the estimated mean hatching date, and October 30, during which time growth was nearly linear.

Given the growth parameters of a stock and the mean annual water temperature, an estimate of M, the instantaneous rate of natural mortality, may be derived by using the relationship provided by Pauly (1980). For male and female silversides, M = 1.31 and 1.32 respectively; thus, about 73% of a silverside year-class dies annually.

REPRODUCTION

Maturation and Condition

Silversides from different sites followed, with minor differences, a similar maturation pattern. In early June, the gonads of most adult females were in the process of maturation or were mature (Nikolsky Classification Stages 3 and 4); few were ready for active spawning (Stage 5; Fig. 8). By June 15-21, small numbers of ripe females were present at all but the site furthest upriver, and by late June (22-28), small numbers of spent females (Stage 6) were recovered at several sites. Most fish were still in the maturation phase. Between June 29 and July 5, most fish were mature, spent fish were more numerous and a few fish with ovaries regressed to the resting stage (Stage 2) were observed. The proportion of spent and resting-stage fish exceeded 80% the following week (July 6-12) according to the visual maturity-stage classification. Almost all fish were in the resting phase by late July and all were by early August.

Temporal changes in maturity index were similar to those of the maturity classification, such that in early June (8-14), the maturity index was highest (mean 15.8, range 7.1-26.8), declining gradually through June as fish spawned (Fig. 9). Less than 30% of females approached maximum ripeness in any week. Spawning was evidently completed by early July, and by early August the maturity index averaged about 1.0. Ovary weights ranged from a June high of 3.23 g in a fish 121 mm long to less than 0.1 g for fish from 98 mm to 117 mm long in early August.

Comparison of the visual classification of gonad maturation state with the calculated maturity index showed that the maturity index increased with increasing maturity state through Stages 3 and 4 (Fig. 10). Considerable overlap in maturity index occurred between Stages 5, 3 and 4 (the states of capacity for active reproduction and increasing and full maturation) because the maturity index is qualitatively incapable of distinguishing between a ripening ovary and one which has shed ova, while the maturation classification system is based on being able to do so with reasonable accuracy. The maturity index then declined markedly through Stage 6, to stabilize at a low value corresponding to Stage 2, the resting stage.

Condition (k) of female silversides remained relatively constant between June 4 and July 24 (SNK - $LSD_{[2-8]} = 0.028$, $P > 0.05$), but showed a significant decline in early August (SNK - $LSD_{[1-3]} = 0.026$, $P < 0.05$) (Table 11). Throughout the spawning period, substantial deposits of adipose tissue were observed in the abdominal cavity. The mean k values did not differ significantly ($P < 0.05$) between sites within a given week. Regression analysis indicated that for fish collected between June 4 and July 24 condition declined significantly ($P < 0.01$) with increasing fish length, even though average condition did not change, such that larger, older, i.e., Age-2 fish had lower condition factors than did the smaller, Age-1 fish ($n = 41$, $k = 0.634 \pm 0.006$ [$\pm$ 95% CI] vs $n = 328$, $k = 0.691 \pm 0.016$). About 20% of the variance of k ($\bar{n} = 369$, $r^2 = 0.20$) can be attributed to differences in fish length.

Fecundity

Absolute fecundity estimates ranged from 1,043 ova in an Age-1 fish 78 mm long to 5,103 ova in an Age-2 fish 117 mm long (Table 12). Fish of similar length varied considerably in fecundity, which increased irregularly with increasing length. The relationship between absolute fecundity and length was described by the GM regression $Y = -2.2025 + 2.8586X$, where $n = 83$, $r^2 = 0.49$, $s^2_{y.x} = 0.0092$, and Y = the logarithm of the absolute fecundity and X = the logarithm of the length in mm.

Ripe and ripening ovaries contained ova of at least two size groups; those of the large size group (> 0.5 mm dried) were considered mature, the others were considered non-mature (Table 13). In ovaries of maximum ripeness (high index of maturity and Maturity Class 4), mature ova averaged 0.75 mm in diameter ($n = 120$, range 0.6 mm-0.9 mm), while non-mature ova averaged 0.38 mm ($n = 120$, range 0.3 mm-0.5 mm). In less mature ovaries, mean ova diameters were smaller still.

Egg retention following spawning was considerable, judging by the size of ovaries following spawning (Fig. 10). The loss of ovary weight (wet) between ovaries ripe and at or near maximum weight (Maturation Class 4) and spent (Maturation Class 6) ranged from 75%-83% for fish between 80 mm and 109 mm long (Table 14). Mature ova (dried) formed about 77% of ovary weight and 55% of total egg numbers, leaving 23% of ovary weight and 45% of numbers as non-mature ova, for fish ($n = 45$) of similar lengths and maturity class (4; maturity index > 20). The proportion of non-mature ova was similar at all lengths of fish.

Estimates of the number of mature ova ranged from 701 in a fish 76 mm long to 3,097 in a fish 117 mm long. The relationship between the number of mature ova and length was described by the GM regression: $Y = -2.5457 + 2.9152X$, where $n = 83$, $r^2 = 0.51$, $s^2_{y.x} = 0.0092$, and Y = the logarithm of the number of mature ova and X = the logarithm of the length in mm. The mean index of maturity of ovaries used in the analysis was 21.2 ± 1.0 ($\pm$ 95% CI). Error in the estimates of the number of mature ova should be negligible, since all were counted; while the error in determining the absolute fecundity should be less than 3%, since the error in estimating the number of non-mature ova was $\bar{x} \pm 6.5\%$ (95% CI) and about 45% of ova were non-mature.

Between early June and early July (much, if not all, of the spawning season) there was no significant difference (SNK - LSD = 6.39, $P > 0.05$) in the absolute fecundity/mm of body length or in the number of maturing or ripe eggs/mm of body length (SNK - LSD = 3.93, $P > 0.05$) for fish of similar mean length (SNK - LSD = 5.3, $P > 0.05$), length range (90 mm-110 mm) and maturity classification (4 and 5) (Table 15).

Sex Ratios

Females were about twice as abundant as males in each age-group. The overall sex ratio for 611 juvenile silversides was 1 male:2.36 females; for 1,281 Age-1 fish, it was 1:1.95 and for 83 Age-2 fish, it was

1:1.86. All ratios were significantly different from 1:1 ($P < 0.01$) but not from 1:2 ($P > 0.05$), and the ratios did not differ significantly between age groups ($\chi^2 = 3.36$, df = 2, $P < 0.05$). Males predominated in the lower estuary (Site 2) throughout June but abruptly declined in abundance in early July (Fig. 11). Some movement upriver to middle-region sites may have occurred by Age-1 males in early June. Evidently few males migrate to the upper reaches of the estuary (Site 5). By mid- to late June, the proportion of males at middle-region sites was declining; and by August, few adults of either sex were found upriver. Females dominated (79%) the composition of a sample collected at the causeway (Site 1) in early August. The scarcity of Age-2 silversides restricts interpretation to the observation that both sexes were most abundant in the middle reaches of the estuary.

DISCUSSION

The abundance of both adult and juvenile Atlantic silversides varied between sampling sites within the Annapolis River estuary and seasonally at each site. During the peak of adult abundance, that is, during the spawning period, adults were most abundant in the middle sections of the estuary, with fewer fish present near the causeway and towards the upstream boundary of the estuary. Large fish tended to be found further upstream than did smaller fish. At the causeway, the low abundance may be a consequence of the lower water temperatures in that area resulting from the turbulent mixing of inflowing tidal waters from the Annapolis Basin. At the site furthest upriver (Site 5), the low abundance may reflect the lack of suitable spawning conditions resulting from low salinity (< 2‰ at depths < 2 m), increased current flow as the channel narrows and the presence of a steep shore with little aquatic vegetation (Middaugh 1981; Middaugh et al. 1981). Site 5 is near the maximum upriver range for silversides, according to Daborn et al. (1979).

The seasonal changes in abundance and distribution of adult silversides are consistent with a pattern of migration into the estuary, probably in April and May, with spawning in June followed by a downriver migration and return to sea between July and October. Most adults leave the estuary soon after spawning, while juveniles begin to migrate from the estuary in September.

Whether any silversides overwinter in the estuary or in the Annapolis Basin is unknown. Any that do may not survive, since the lower lethal temperature for silversides is 1°-2°C (Hoff and Westman 1966; Conover and Murawski 1982), and these temperatures are reached upriver of the causeway, where winter ice cover is normal, and in the basin (pers. comm., G. Irbe, Atmospheric Envir. Serv.). However, since silversides are reportedly present under the winter ice in Malpeque Bay, Prince Edward Island (Needler 1940), the lethal temperature may be somewhat lower for northern populations, thus permitting overwinter survival.

Conover and Murawski (1982) conclude that populations of silversides "north of Cape Hatteras undergo an offshore winter migration from inland to inner continental shelf waters" where they remain within about 50 km of shore and the 100-m depth contour. In Cumberland Basin, Bay of Fundy, silversides were absent between December and March from inshore areas (pers. comm., I. Salinas, Dept. of Biology, Dalhousie University). However, in some areas a small proportion of silversides may remain inshore, since Bigelow and Schroeder (1953) report anecdotally that they are resident throughout the year wherever found in southern New England and, as previously noted, are said to be found beneath the winter ice in Prince Edward Island. The presence or absence of silversides during winter seems to depend upon the prevailing environmental conditions. Thus most, if not all, of the silverside population from the Annapolis River probably moves into the Bay of Fundy and perhaps as far as the banks off southern Nova Scotia. Winter temperatures in the Bay of Fundy range from 1°-2°C at depths less than about 150 m (Fish and Johnson 1937) and are similar in the Annapolis Basin (pers. comm., G. Irbe, Atmospheric Envir. Serv.).

Statistical analysis of the sample length data for adult and juvenile silversides was complicated by the fact that it did not meet the assumptions of some of the methods used. Such non-compliance is frequent in field data and can be remedied in several ways, according to the particular problem (Green 1979). Glass et al. (1972) conclude that the concern is not whether "assumptions are met exactly, but rather, whether plausible violations of the assumptions have serious consequences on the validity of probability statements". For reasons previously noted, the consequences in this study of not fully meeting these assumptions is believed not to be serious.

Silversides from the Annapolis River, which is near the northern limit of their range (Leim and Scott 1966), have a higher maximum age and higher proportion of older fishes than do more southerly populations. Thus, the proportion of Age-2 fish increases from zero in Chesapeake Bay (Bayliff 1950), to a marginal presence in Massachusetts (Conover and Ross 1982), to over 6% in the Annapolis River. The absence of two-year-old fish in the commercial catch from Prince Edward Island (Jessop and Morantz 1982) can be attributed to the time of sampling (the older fish had probably departed inshore areas by early October) and perhaps to effects of the fishery.

Age-0 silversides attain, by September 30, average sizes that decrease from south to north while average growth rates increase. In Chesapeake Bay, total lengths average approximately 90 mm (Bayliff 1950), in Massachusetts, about 86 mm (Conover and Ross 1982) and in the Annapolis River, only 79 mm. Observed summer-autumn growth rates (TL) for Age-0 silversides (sexes combined) from the Annapolis River were about 23 mm/month, as compared with 20 mm/month in Essex Bay, Massachusetts (Conover and Ross 1982) and 10 mm-15 mm/month in Long Island Sound (Austin et al. 1973, cited in Conover and Ross 1982); although Barkman et al. (In press) report a growth rate of about 25 mm/month in Narragansett Bay, Rhode Island. These growth-rate differences may stem from environmental differences. More rapid growth in the Annapolis River could result from warmer water temperatures in the temperature- and salinity-stratified headpond than in the shallow marsh-bay complex of Essex Bay where a high tidal amplitude precludes stratification (Jessop 1976; Conover and Ross 1982; Bengtson 1981). A shorter northern growing season seems to be the primary factor accounting for the decreasing average size of Age-0 silversides from south to north.

Growth ceases during the winter in populations at latitudes between Chesapeake Bay and Prince Edward Island and the annual marks found on silverside scales represent post-spawning checks laid down between May and July, depending upon the latitude (Bayliff 1950; Conover and Ross 1982; Jessop and Morantz 1982).

Although the maximum lengths of adult silversides are similar from south to north, e.g., maximum observed total lengths of 137 mm in the Annapolis River, 140 mm in Massachusetts (Conover and Ross 1982) and Chesapeake Bay (Bayliff 1950), the southern fish are Age 1 while the northern fish are Age 2. Bayliff (1950) noted that females were larger than males at maturity but size differentiation clearly begins in the late summer of the first growing season. Conover and Ross (1982) report a similar finding.

Growth rates differed for silversides located in different regions of the estuary. Higher growth rates occurred at middle-region sites, having large, gently sloped beaches with moderate wave action and little current. Growth rate differences may be a result of productivity differences within the variety of biological communities found in the estuary, some of which are more suited to supporting an abundance of silversides than are others. Differences in juvenile growth rates in different sectors of a habitat were also reported by Ridenhour (1960). These differences also imply that both adult silversides, prior to their post-spawning emigration, and juveniles have a home range of limited size. A tagging study of limited scope by Butner and Brattstrom (1960) supports the concept of localized patterns of movement by schools of silversides, as does the observation that juvenile silversides tend to remain in the area of hatching until about 50 days old, after which their mobility increases (Barkman et al. 1978). Conclusions unrepresentative of the entire population could result from the use of growth data collected from only one site, particularly for juvenile silversides.

Alternatively, adult silversides, following spawning, and juvenile silversides might range widely within the estuary, with fish segregating by size and tending to concentrate in different areas at different times. It is difficult to envisage how or why this more complex behaviour pattern might occur in a manner consistent with the observed results. A study of the seasonal movements of silversides within a variety of estuarine morphologies, perhaps by tagging, would be enlightening.

The asymptotic size should generally provide good agreement between values of L_{max} and L_∞ in small fishes when the underlying data are good ($L_{max} \simeq 0.95\ L_\infty$; Taylor 1958), and such is the case here. Estimates of L_∞ for Annapolis River silversides were lower than for Massachusetts silversides (males 130 mm total length, females 136 mm vs 139 mm and 146 mm), the parameter values for which were obtained using data from Conover and Ross (1982). The ratio L_{max}/L_∞ (sexes combined) was slightly higher for Annapolis River silversides (1.0) than for those from Massachusetts (0.95), whose lower value might result from a higher mortality rate implied by the absence or near absence of Age-2 fish in the more southern population. The ratio L_m/L_∞ (sexes combined), where L_m is the length at first reaching maturity, was similar for silversides from the Annapolis River (0.70) and Massachusetts (0.68) as expected, since this ratio is constant within a family (Beverton 1963). The relatively high value of this ratio and the low (1.3) value of the ratio of M/K indicates a high reproductive load for silversides.

The higher K values for silversides are characteristic of fast-growing fishes (Beverton and Holt 1959). The K values (3-parameter VBGF) for Massachusetts silversides (1.24 for males, 1.39 for females) are higher than for Annapolis River fish (1.00 and 1.04, respectively), relfecting their higher mortality rates and shorter life span, yet similar maximum size.

Growth functions typically assume that growth is a continuous process, whereas it normally is a discontinuous process, with growth rates varying seasonally in response to environmental factors such as water temperature and food availability (Weatherly 1972). Recognition of the seasonal variability in silverside growth is useful for its realism and for the assistance it may provide in understanding the underlying environmental relationships. Although the 3-parameter VBGF is commonly fitted to fisheries data, a better fit and more realistic parameter values are obtained from the 4-parameter version and, for species such as silversides which have short life spans and experience seasonal growth, accounting for seasonal growth results in a still better fit. The differences in parameter estimates, particularly L_∞ and k, derived from the various procedures, have practical implications in the assessment of population dynamics and the study of life-history strategies (Gaschütz et al. 1980; Estes 1979; Adams 1980).

The high estimates of M, the coefficient of natural mortality, obtained from the Pauly (1980) relationship are consistent with the observed proportion of Age-2 silversides (6.1%), since it predicts a survival of 7.3% to Age 2. The high M value for silversides is also consistent with their high gonad-maturity index, the relationship being similar to that for capelin (Gunderson 1980). To summarize, the high values of K, M and the ratio L_m/L_∞ are characteristic of fishes which grow quickly and die young.

Expected values of Y ($\hat{Y}$), calculated from the length-weight and fecundity-length relationships for some X value, will underestimate the arithmetic mean of actual observed Y values at X, because the Y values are geometric means (GM) rather than arithmetic means (AM) and can be corrected by using the formula given on page 275 of Ricker (1975). Comparison of uncorrected and corrected values indicates that the error for the length-weight relationship is less than 0.8% and for the fecundity-length relationship is less than 2.4%. The method of selection of pairs of variates for these relationships results in a bias of the slope of the functional regression towards underestimation, but this bias should be minor in view of the large sample size per interval and the high coefficient of determination. Ideally, half of the pairs of variates should have been chosen on the basis of X intervals and half on the basis of Y intervals (Ricker 1973).

Good approximation may be obtained for confidence intervals about the regressions and for point estimates by using ordinary symmetrical confidence limits; although, strictly, they are not valid (Ricker 1973). Where the coefficients of determination are high, as they are here, the errors become negligible.

Although spawning by silversides was not observed in the Annapolis River, inferences can be made about the process. Temporal changes in maturity state and maturity index indicated that most spawning occurred between June 8 and July 5. Daily water temperatures during this period exceeded 12°C and frequently exceeded 16°C (Fig. 12), which may be the minimum temperature required for spawning (Middaugh and Lempesis 1976; Middaugh 1981). Water temperatures in the Annapolis River typically reach about 14°C by early June (Envir. Canada 1976); thus spawning is unlikely in May in an average year. In 1982, positively identified silverside eggs were collected from Site 4 on June 11. The mid-river water temperature was 16°C, and inshore it was somewhat warmer in the vegetation where the eggs were collected. The eggs were in the early to late eyed stage and when kept in a container at room temperature, hatched 5-6 days later. Spawning also occurs in June in Prince Edward Island (Needler 1940). Timing and duration of spawning tends to vary with latitude, being earlier and longer in more southern populations (Robbins 1969). For example, in North Carolina, ripe fish have been found from March through August (Hildebrand 1922); while in Massachusetts, they were collected during May through July at water temperatures from 13°C-21°C (Kendall 1901).

The bimodal, juvenile length distributions evident in certain of the August 18-19 and later samples (Fig. 4) imply the occurrence of at least two spawning periods. The skewed, unimodal distributions of earlier samples can be attributed to the inefficiency of the seine in collecting fish less than about 25 mm long, resulting in an underestimate of the abundance of fish spawned in late June. Observation and non-quantitative collections with the use of a fine-meshed dip net at Sites 1, 2 and 4 on July 8 and 9 revealed abundant silversides with lengths from 9 mm to 16 mm, suggesting spawning activity in late June. The single mode of larger juveniles collected at all sites in late July implies further spawning activity in early to mid-June. In South Carolina, spawning occurs in the upper intertidal zone during daylight high tides, near the time of the new and full moons (Middaugh 1981). New and full moons occurred on June 12 and 28, respectively, in 1980.

It is unknown whether individual silversides in the Annapolis River spawn just once during a season or are fractional spawners over a short or long period. The hypothesis of a single spawning beat (or several beats within a short, i.e., 2-3 day, period) by an individual female is supported by the presence of two modes in the egg-diameter- frequency histogram of ripe fish, in which the group of larger-diameter eggs forms about 77% of ovary weight, a figure similar to the loss of ovary weight between maturity Class 4 (ovaries ripe and at or near maximum weight) and Class 6 (ovaries spent). Also, there is no decline throughout the spawning season in the number of ova/mm of body length of ripe fish, as would be expected if multiple spawnings of individual fish occurred. A single spawning by each female, with individuals ripening over a comparatively short spawning period, may be an adaptation to the shorter growing season and more fluctuating environmental conditions found near the northern limit of the silversides' range.

Different spawning patterns are reported for southern populations of silversides. Conover (1979) concludes that silversides in Massachusetts are fractional spawners over an extended period and Hildebrand (1922) suggests that individuals spawn more than once annually in the southern portion of their range.

Maturation and first spawning by silversides occurs at Age-1 in the Annapolis River and throughout their geographic range (Bayliff 1950; Conover and Ross 1982). Since body condition factors (k) and maturity indices are relatively low during April in a New England silverside population and condition factors increase during the time that gonad maturation occurs (Conover 1979; Conover and Ross 1982), it is reasonable to conclude that similar events occur in Nova Scotian populations. During this process, ovary weights may increase by as much as 300 times. Prior to and during the spawning period, the high and relatively constant body condition of most fish is a reflection of the abundant food supply at this time, as attested by their full stomachs and substantial deposits of abdominal adipose tissue. Age-1 female silversides from Annapolis River and from Massachusetts (Conover and Ross 1982) had similar condition factors in early August (0.54 vs 0.52, based on total lengths), but between June and August, condition declined with length for Annapolis River silversides, such that Age-2 fish had lower condition factors than did Age-1 fish. The lower condition, if maintained, could contribute to the overwinter mortality of Age-2 fish, none of which evidently survive to spawn again.

Fecundity increased with silverside length, weight and age. Depending upon fish length, the numbers of mature, presumably spawnable ova, i.e., the fertility, ranged from 700 to 3,100. Any trends in fecundity with latitude are obscured by the imprecision of the scant available data. Estimates of the number of mature ova range from about 500 for an average-size female in North Carolina (Hildebrand 1922), to about 300 mature (with many smaller atretic ova) in Chesapeake Bay (Bayliff 1950), to 300-1,000 (average 500) in New England waters (Barkman and Beck 1976). No information is given as to how these numbers were derived; they seem to be based on single strippings of ripe females. These figures undoubtedly underestimate true fertility, since, as noted previously, individual silversides may spawn more than once annually in the southern portion of their range. Also, the difference, i.e., egg retention, between absolute fecundity and fertility may vary between populations of the same species, although it was similar (45% vs 46%, respectively) between silversides of similar total lengths from the Annapolis River and Massachusetts (Conover 1979). Inter-population comparisons are perhaps best made on the basis of absolute fecundity, in which case mid-latitude (Massachusetts) silversides have a higher fecundity (4,725-13,525 ova/female) than do those from northern latitudes (Annapolis River, 701-3,097 ova/female). A higher fecundity in more southern, semelparous populations may be a consequence of the allocation of more energy to post-reproductive reserves by iteroparous, northern populations, thereby ensuring their successful return migration to the sea (Glebe and Leggett 1981).

In and Annapolis River, Age-2 silversides make an important contribution to population fertility, because perhaps 6% of the spawning stock contributes about 10% of the total egg deposition. The reciprocal trends in relative fecundity and frequency of reproduction between northern and southern populations of shad and other species tends to reduce differences in mean lifetime fertility, and may represent genetically based adaptations to their environments (Leggett and Carscadden 1978). Such may also be the case for silversides.

Females were about twice as abundant as males in each age group. On Prince Edward Island, females also significantly outnumbered males at Age 1 but did not at Age 0 (Jessop and Morantz 1982); while in more southern populations, the sex ratios were approximately equal (Hildebrand 1922; Bayliff 1950; Conover and Ross 1982). As Nikolsky (1963) notes, it is not unusual for the sex ratios to differ between populations of the same species. An intriguing explanation of the high proportion of female silversides observed in the Annapolis River is offered by Conover and Kynard (1981), who have demonstrated that the sex determination of silversides is under genetic and temperature-dependent environmental control during a critical phase of larval development. Thus, under a cold, fluctuating temperature regime, such as occurs in the Maritime Provinces, a high proportion of females result. The seasonal variation in juvenile silverside sex ratios occurring in Massachusetts could not be confirmed in the Annapolis River because most fish were not sexed prior to August and the attainment of a length of about 65 mm.

Atlantic silversides are of commercial value but are generally unutilized (Bayliff 1950; Jessop and Morantz 1982). Nonetheless, the development of active commercial fisheries such as the one in Prince Edward Island (Jessop and Morantz 1982) usually results in a requirement for management advice. Insights may be gained into the consequences for fisheries management of the life history of the silverside by viewing the species in terms of r- and K-selection theory (Adams 1980). Silversides are typical r-strategists, with their life history characterized by small body size, low maximum age, low age at first maturity, high natural mortality rate (M) and high growth rate (K), a high allocation of available energy resources to reproductive activities, as evidenced by a high gonad maturity index, and semelparity rather than iteroparity (Estes 1979; Adams 1980; Gunderson 1980). The r-selection strategy is an adaptation to a variable and/or unpredictable environment such as an estuary, where mortality tends to be density independent and catastrophic mortalities occasionally occur. In northern populations of silversides, a longer life span, mild iteroparity and reduced fecundity might indicate that fluctuations in juvenile mortality play a greater role than in southern populations, where environmental conditions are more stable (Murphy 1968; Schaffer 1974).

Adams (1980) states that fisheries based on more r-selected species will be more productive and such species can be fished at younger ages and at higher levels of exploitation than can K-selected species. Such fisheries are likely to be of a boom and bust nature because of erratic fluctuations in production levels but, given a minimum population size, should also recover quickly from overfishing. The probabilisitc life-history strategies of r-selected species, e.g., for spawning, may also make them less vulnerable to any detrimental effects of exploitation on the maintenance of stock genetic variability (MacLean and Evans 1981). These guidelines are, of course, quite general and effective management would require specific information from a developing fishery.

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TABLE 1. Linear contrasts, between age-sex groups, of the mean lengths (mm) of Atlantic silversides from the Annapolis River, 1980. (Sites 2, 3, 4, 5 combined; df = 1,285.)

Contrast	t-value	Probability
Age 1 vs Age 2	394.6	<0.0001
Male vs female	-86.5	<0.0001
Interaction	-63.9	<0.0001

TABLE 2. Covariance analysis of the temporal changes in lengths (mm) of adult Atlantic silversides, by age-sex group, between sites in the Annapolis River, 1980.

Source of variation	df	Sum of squares	Mean square	F	Probability
Male, Age 1[1]					
Equality of adjusted means	3	165.6	55.21		
Zero slope	1	1,084.9	1,084.93		
Error	417	20,155.7	48.34		
Equality of slopes	3	489.5	1,631.18	3.44	0.017[2]
Error	414	19,666.2	47.50		
Total	421	21,406.3			
Female, Age 1[1]					
Equality of adjusted means	3	275.9	91.97		
Zero slope	1	10,649.7	10,649.75		
Error	783	32,067.1	40.95		
Equality of slopes	3	1,222.4	407.46	10.30	< 0.001
Error	780	30,844.7	39.54		
Total	787	42,992.8			
Male, Age 2[3]					
Equality of adjusted means	2	32.2	16.08	0.53	0.596
Zero slope	1	74.8	74.80	2.46	0.130
Error	24	728.6	30.36		
Equality of slopes	2	5.4	2.71	0.08	0.921
Error	22	723.2	32.87		
Total	27	835.5			
Female, Age 2[3]					
Equality of adjusted means	2	26.9	13.47		
Zero slope	1	0.3	0.33		
Error	45	1,138.9	25.31		
Equality of slopes	2	214.6	107.31	4.99	0.011
Error	43	924.3	21.50		
Total	48	1,166.2			

[1]Age-1 data from Sites 2, 3, 4, 5.
[2]When this test is significant, further tests are inappropriate.
[3]Age-2 data from Sites 2, 3, 4, there being insufficient Age-2 fish at Site 5.

TABLE 3. Comparison between sites of the age-sex group regression statistics from the covariance analysis of the lengths (mm) versus sampling date of adult Atlantic silversides from the Annapolis River, 1980.

Site[1]	n	Slope	SE	Prob.[2]	Intercept	SE	r^2
Male, Age 1							
2	131	0.193	0.038	< 0.001	79.82	1.350	0.40
3	108	0.112	0.045	0.006	82.84	1.260	0.07
4	167	0.029	0.037	0.440	85.22	0.858	< 0.01
5	16	0.025	0.106	0.810	82.50	2.037	0.04
1-5 combined	434	0.130	0.019	< 0.001	82.69	0.586	0.10
Female, Age 1							
2	163	0.322	0.024	< 0.001	82.05	1.106	0.53
3	286	0.259	0.025	< 0.001	84.86	0.880	0.27
4	215	0.075	0.036	0.040	90.07	0.871	0.02
5	124	0.241	0.055	< 0.001	86.62	0.917	0.14
1-5 combined	847	0.267	0.011	< 0.001	85.43	0.405	0.41
Male, Age 2							
2	7	0.033	0.407	> 0.750	108.94	8.559	0.01
3	9	0.165	0.208	0.450	107.39	5.774	0.08
4	12	0.087	0.062	0.190	110.57	2.219	0.17
1-5 combined	29	0.100	0.056	0.080	109.20	1.652	0.11
Female, Age 2							
2	11	0.144	0.061	0.040	110.23	3.004	0.39
3	27	-0.112	0.056	0.060	118.75	1.647	0.14
4	11	0.004	0.117	> 0.750	114.27	3.142	< 0.01
1-5 combined	54	0.074	0.036	0.040	113.67	1.286	0.08

[1] Site-1 data included in combined data but not analysed separately because of small sample size.

[2] Probabilities based on F values from ANOVA for testing $H_O: B = 0$.

TABLE 4. Comparison[1] between sites of the slopes of the regressions of length versus date for age-sex groups of adult Atlantic silversides from the Annapolis River, 1980.

Age-sex group	Slope (site)			
Male, Age 1	0.025 (5)	0.029 (4)	0.112 (3)	0.193 (2)
Female, Age 1	0.075 (4)	0.241 (5)	0.259 (3)	0.322 (2)
Male, Age 2	0.033 (2)	0.087 (4)	0.165 (3)	
Female, Age 2	-0.112 (3)	0.004 (4)	0.145 (2)	

[1] A posteriori comparisons based upon the simultaneous test procedure (Sokal and Rohlf 1969). Significance established at $P < 0.05$.

TABLE 5. Comparison of the adjusted age-sex group mean lengths (mm) between sites on several dates for adult Atlantic silversides from the Annapolis River, 1980. (Site numbers in parentheses.)

Date	Adjusted mean lengths (mm)				$Q_{.05} S_{\bar{X}}$[1]
Male, Age 1					
June 1	80.02 (2)	82.53 (5)	82.96 (3)	85.25 (4)	D_4 = 3.69 D_3 = 3.37 D_2 = 2.81
July 1	83.28 (5)	86.01 (2)	86.10 (4)	86.31 (3)	
July 15	83.64 (5)	86.50 (4)	87.87 (3)	88.49 (2)	
Female, Age 1					
June 1	82.37 (2)	84.89 (3)	86.86 (5)	90.13 (4)	D_4 = 1.74 D_3 = 1.59
July 1	92.04 (2)	92.37 (4)	92.67 (3)	94.10 (5)	
July 15	93.41 (4)	96.29 (3)	96.54 (2)	97.48 (5)	
Male, Age 2					
July 1[2]	110.49 (2)	112.05 (3)	113.20 (4)		D_3 = 6.52
Female, Age 2					
June 1	110.37 (2)	114.27 (4)	118.64 (3)		D_3 = 4.66 D_2 = 3.89
July 1	114.39 (4)	114.71 (2)	115.27 (3)		
July 15	114.40 (4)	114.82 (3)	115.28 (2)		

[1]$S_{\bar{X}}$ based on harmonic mean of m samples.
[2]Based on common slope for Sites 2, 3, 4.

TABLE 6. Covariance analysis of the lengths (mm) of adult Atlantic silversides, by age-sex group (Sites 1 to 5 combined), in the Annapolis River, 1980.

Source of variation	df	Sum of squares	Mean square	F	Probability
Equality of adj. cell means	3	55,173.0	18,391.01		
Zero slope	1	24,681.1	24,681.10		
Error	1,359	60,683.2	44.65		
Equality of slopes	3	2,511.3	837.09	19.51	< 0.001[1]
Error	1,356	58,171.9	42.90		
Total	1,363	140,537.3			

[1]When this test is significant, further tests are inappropriate.

TABLE 7. Comparison between age-sex groups of the regression slopes and adjusted mean lengths (mm) of adult Atlantic silversides from the Annapolis River, 1980. (Sites 1-5 combined.)

Statistic/slope[1]	Value (Age-sex group)			
	0.074 (F2)	0.100 (M2)	0.130 (M1)	0.267 (F1)
Adjusted means at June 1[2]	82.82 (M1)	85.69 (F1)	109.30 (M2)	113.75 (F2)
July 1	86.60 (M1)	93.44 (F1)	112.20 (M2)	115.88 (F2)
July 15	88.55 (M1)	97.45 (F1)	113.71 (M2)	116.98 (F2)

[1]A posteriori comparisons based upon simultaneous test procedure (Sokal and Rohlf 1969). Significance established at $P < 0.05$.

[2]$Q_{0.05}S_{\bar{x}} = 2.86$ where $S_{\bar{x}}$ was based on the harmonic mean X_m of 4 age-sex groups.

TABLE 8. Analysis of variance, by sample date ($\log_{10}$ transformed) of the lengths (mm) of juvenile Atlantic silversides from the Annapolis River, 1980.

Source	df	SS	MS	F	Probability
Site 1					
Among dates	4	37,951.1	9,487.77	103.82	<0.001
Linear regression	1	21,459.9	21,459.86	234.82	<0.001
Polynomial degree 2	1	12,921.5	12,921.50	141.39	<0.001
Residual	2	3,569.7	1,784.85	19.53	<0.001
Within dates	344	31,439.5	91.39		
Total	348	69,390.6			
Site 2					
Among dates	4	102,451.3	25,612.83	155.08	<0.001
Linear regression	1	99,454.0	99,454.04	602.17	<0.001
Residual	3	2,997.3	999.09	6.05	<0.001
Within dates	344	56,814.1	165.16		
Total	348	159,265.4			
Site 3					
Among dates	4	29,473.5	7,368.37	67.78	<0.01
Linear regression	1	26,823.4	26,823.42	246.74	<0.01
Residual	3	2,650.1	883.36	8.13	<0.01
Within dates	299	32,504.1	108.71		
Total	303	61,977.6			
Site 4					
Among dates	5	106,073.1	21,214.63	231.17	<0.001
Linear regression	1	100,880.2	100,880.25	1,099.27	<0.001
Residual	4	5,192.9	1,298.22	14.15	<0.001
Within dates	379	34,780.9	91.77		
Total	384	140,854.1			
Site 5					
Among dates	5	64,979.2	12,995.84	128.85	<0.01
Linear regression	1	62,883.6	62,883.64	622.98	<0.01
Residual	4	2,145.6	536.39	5.32	<0.01
Within dates	278	28,038.5	100.86		
Total	283	93,017.7			
Sites 1-5					
Equality of slopes[1]	4	311,451.1	77,861.78	607.03	<0.001
Residual error	1,661	213,054.3	128.27		

[1]Linear regression.

TABLE 9. Comparison between sites of the regression statistics from the analysis of variance of the lengths (mm) versus sampling date ($\log_{10}$ transformed) of juvenile Atlantic silversides from the Annapolis River, 1980.

Site	n	Slope	SE	Intercept	SE	r^2
1	349	37.461	3.005	-10.395	5.109	0.31
2	349	135.498	5.641	-199.435	10.796	0.62
3	304	74.398	4.901	-87.770	9.336	0.43
4	385	104.671	3.367	-146.313	6.334	0.72
5	284	95.405	3.938	-128.069	7.563	0.68

Slopes[1]

37.46 (1)[2]	74.40 (3)	95.41 (5)	104.67 (4)	135.50 (2)

(74.40 (3), 95.41 (5) and 104.67 (4) are joined by a common underline.)

[1]A posteriori comparisons based upon simultaneous test procedure (Sokal and Rohlf 1969). Significance established at $P < 0.05$.

[2]Sites in parentheses.

TABLE 10. Estimates of von Bertalanffy growth-function parametes (fork lengths in mm and time in months) for Atlantic silversides from the Annapolis River, 1980.

Function form	Sex	L_∞	K	t_0	D	ts	C	r^2
3-parameter	M[1]	122.2[2]	1.00	-0.348	1.0	-	-	0.978
	F	128.2	1.04	-0.305	1.0	-	-	0.985
3-parameter seasonal	M	124.4	1.05	-0.418	1.0	0.221	2.12	0.999
	F	130.7	1.09	-0.371	1.0	0.217	2.01	0.999
4-parameter	M	122.3	1.20	-0.421	0.86	-	-	0.982
	F	128.3	1.26	-0.380	0.85	-	-	0.987
4-parameter seasonal	M	123.1	1.34	-0.441	0.86	0.209	2.10	0.999
	F	129.5	1.39	-0.416	0.85	0.213	2.03	0.999

[1]Calculations are based on 22 data pairs for males, 26 for females.

[2]Equivalent total length values for the 3-parameter VBGF are: 130.0, 136.4; 132.5, 139.0 mm.

TABLE 11. Weekly mean condition (k), between June 4 and August 6, of female Atlantic silversides from the Annapolis River, 1980.

Date	n[1]	k			Length (mm)	
		Mean	SD	Range	Mean	SD
Jun 1-7	43	0.687	0.047	0.55-0.77	93.6	11.21
Jun 8-14	51	0.674	0.056	0.57-0.81	93.5	8.68
Jun 15-21	70	0.686	0.052	0.58-0.81	98.2	11.84
Jun 22-28	41	0.683	0.058	0.52-0.83	92.6	6.95
Jun 29-Jul 5	71	0.689	0.048	0.56-0.78	94.3	7.85
Jul 6-12	57	0.687	0.054	0.54-0.78	97.1	8.93
Jul 20-26	34	0.678	0.046	0.62-0.78	101.9	5.83
Aug 6	23	0.640	0.054	0.50-0.74	109.1	6.42

[1]All samples except that of August 6 are composites from several upriver sites; the August 6 sample is from Site 1.

TABLE 12. Fecundity, by length group, of Atlantic silversides from the Annapolis River, 1980.

Length interval (mm)	n	Total number of ova			Number of mature ova		
		Mean	SD	Range	Mean	SD	Range
75.0-79.9	6	1,877	877.8	1,043-3,414	1,202	591.7	701-1,985
80.8-84.9	9	1,855	315.1	1,459-2,367	1,145	145.6	962-1,368
85.0-89.9	16	2,524	492.0	1,838-3,586	1,292	234.6	818-1,701
90.0-94.9	15	2,643	620.0	1,781-3,805	1,685	400.9	1,096-2,767
95.0-99.9	16	3,039	502.8	2,078-3,924	1,688	330.2	1,206-2,223
100.0-104.9	12	3,282	474.7	2,374-4,224	2,024	270.7	1,727-2,590
105.0-109.9	2	3,308	-	2,777-3,838	1,825	-	1,784-1,865
110.0-114.9	3	3,851	980.6	3,190-4,978	2,435	360.6	2,137-2,836
115.0-119.9	3	3,738	1,212.2	2,787-5,103	2,332	739.9	1,620-3,097
120.0-124.9	1	4,661	-	-	2,640	-	-

TABLE 13. Percent frequency of egg diameters (dried) for Atlantic silversides from the Annapolis River, 1980[1]

Sample	Fork length (mm)	Index of maturity	Maturity class	Fecundity	Egg diameter (mm)							
					0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
1	89	12.5	3	1,975	-	30.1	4.3	6.6	47.3	11.8	-	-
2	92	12.0	3	2,250	1.3	21.5	2.5	7.5	54.2	13.1	-	-
3	92	13.9	3	1,896	4.3	26.5	3.4	-	51.0	14.8	-	-
4	91	25.7	4	3,093	-	15.1	23.2	8.1	2.7	38.9	12.1	-
5	95	23.9	4	2,593	-	22.5	20.0	7.5	-	8.8	31.2	10.0
6	96	26.8	4	3,924	-	13.0	17.3	11.9	5.4	29.7	21.2	1.4

[1]Percent frequencies based on subsamples of 40 ova from each of the > 500-μ and < 500-μ fractions of total fecundity.

TABLE 14. Comparison of mean fresh ovary weights (g) of ripe unspawned and spent ovaries (Maturity Classes 4 and 6, respectively) from Atlantic silversides from the Annapolis River, 1980.

Maturity class	Fork length interval (mm)								
	80-89			90-99			100-109		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
4	17	1.28	0.226	16	1.67	0.242	11	2.00	0.254
6	9	0.29	0.163	19	0.42	0.152	10	0.35	0.160
% difference	77			75			83		

TABLE 15. Temporal patterns in the number of ova/mm of body length of female Atlantic silversides from the Annapolis River, 1980.

Date	Sample size	Total eggs/mm		Mature eggs/mm		Fish length (mm)	
		$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Jun 4-5	23	29.5	6.26	18.2	3.46	96.1	4.95
Jun 9-11	10	31.8	5.58	17.3	2.62	97.5	4.55
Jun 16-18	7	32.8	5.19	19.4	5.11	98.3	4.11
Jun 23-Jul 8	5	31.5	3.09	20.4	2.60	96.6	5.22

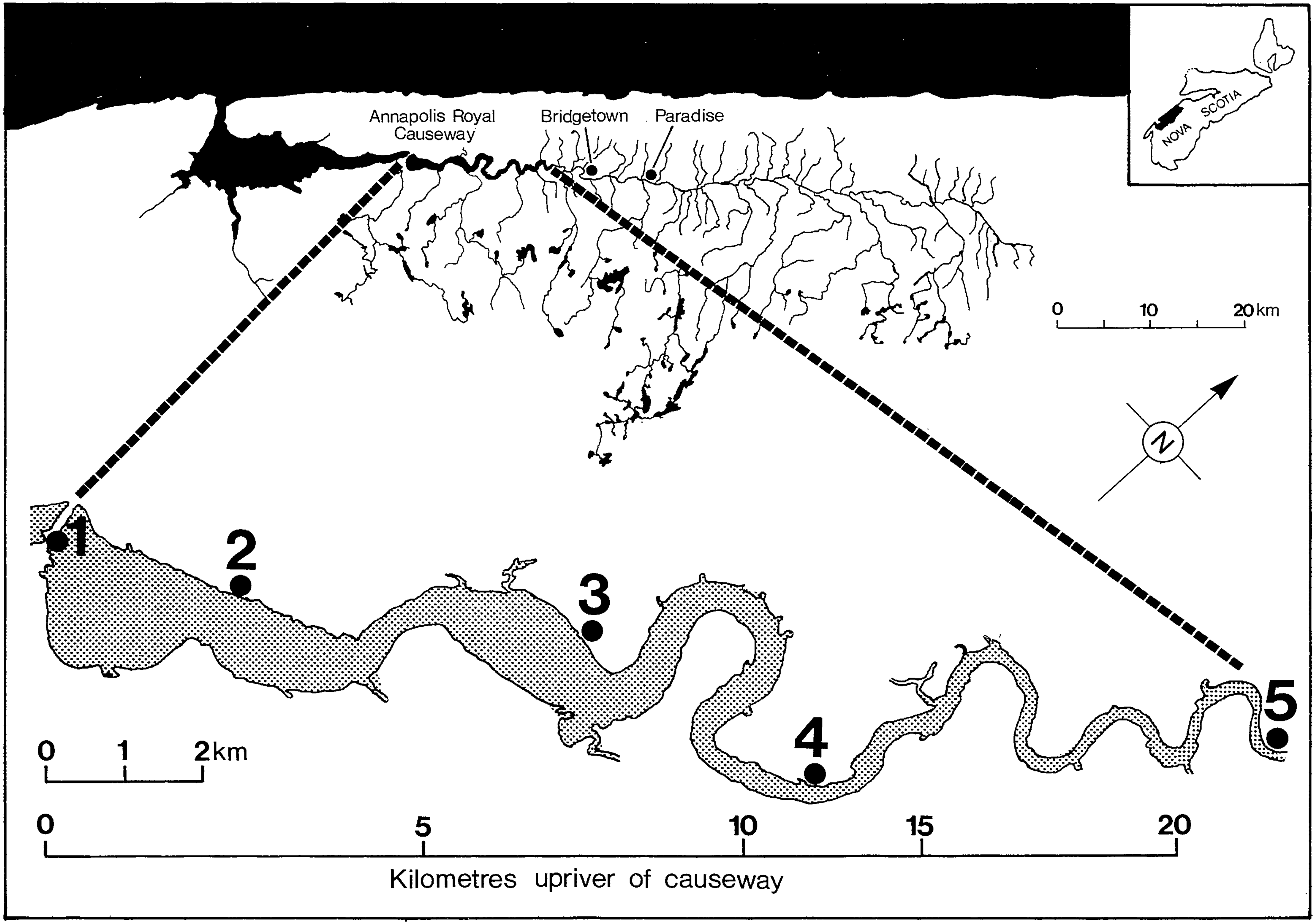

FIG. 1. The Annapolis River system.

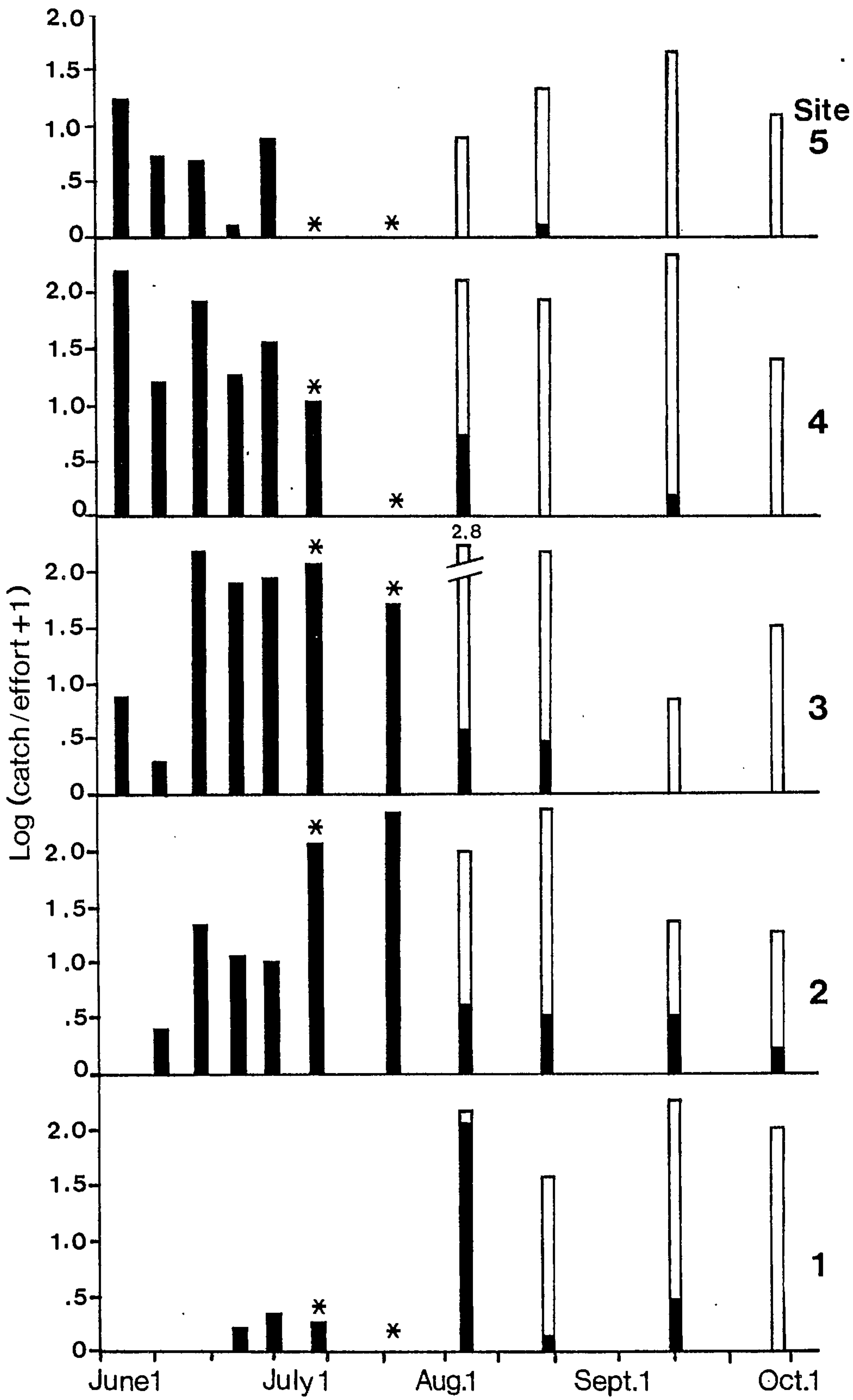

FIG. 2. Catch per seine haul of Atlantic silversides from five sites in the Annapolis River, 1980.

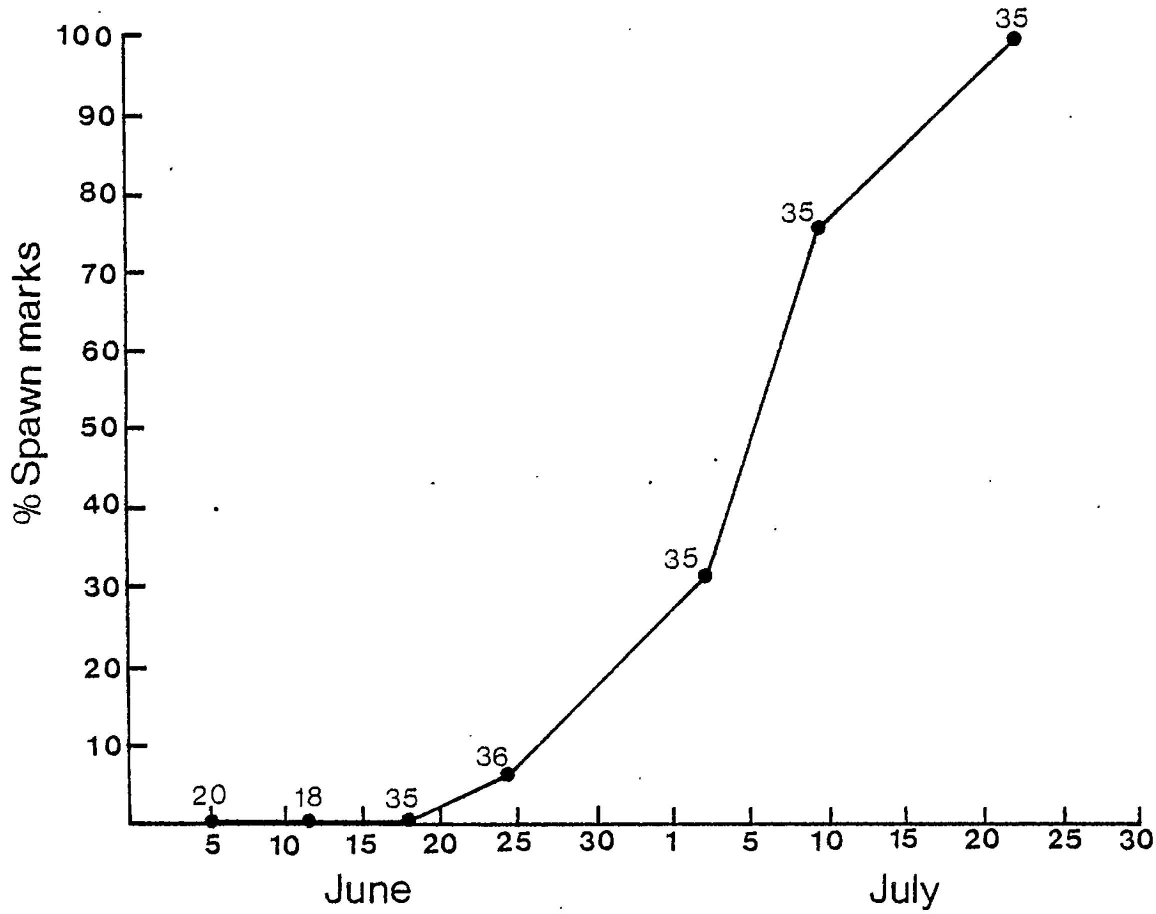

FIG. 3. Temporal development of annuli on scales of Atlantic silversides from the Annapolis River, 1980.

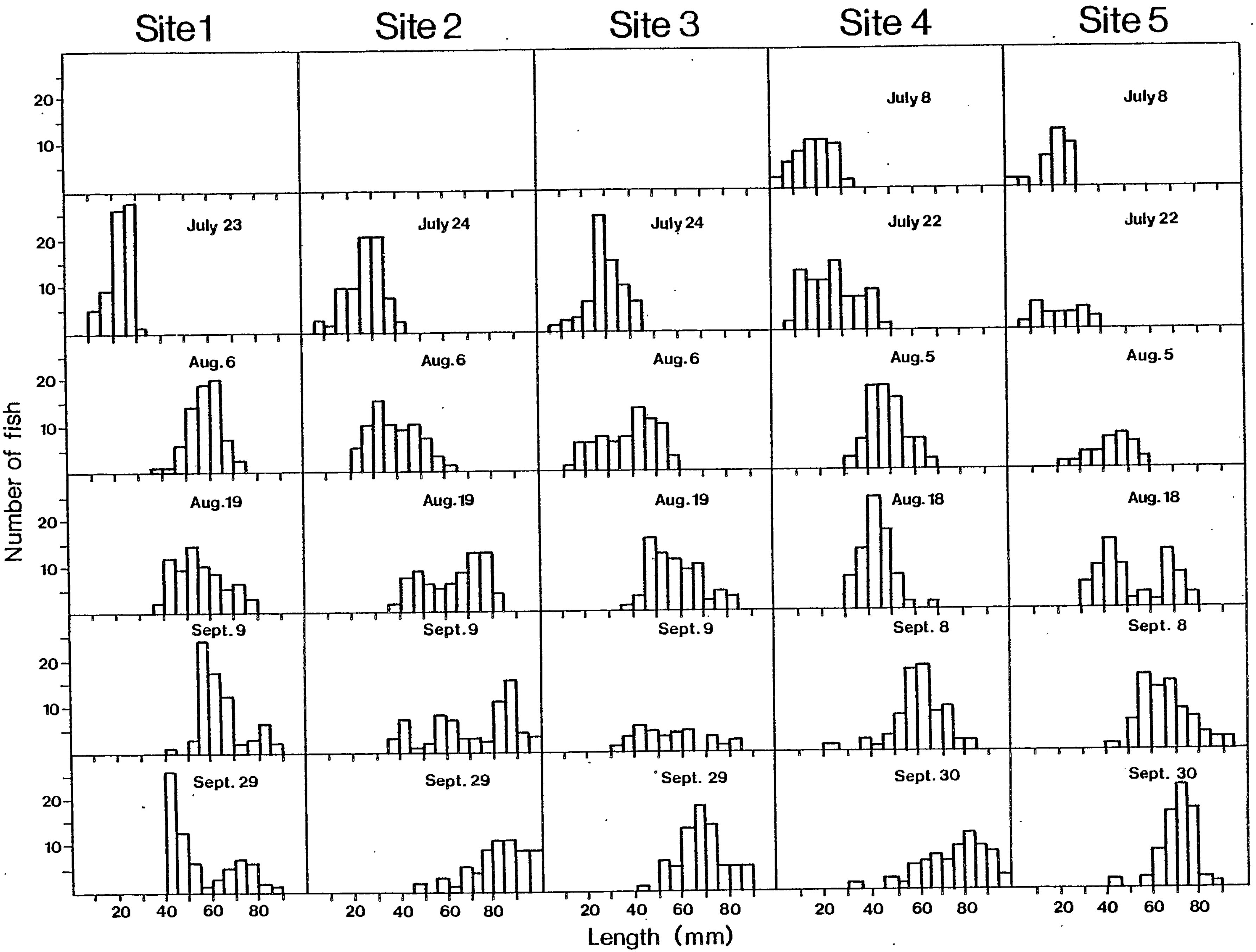

FIG. 4. Length-frequency histograms of the sample data for juvenile Atlantic silversides from the Annapolis River, 1980.

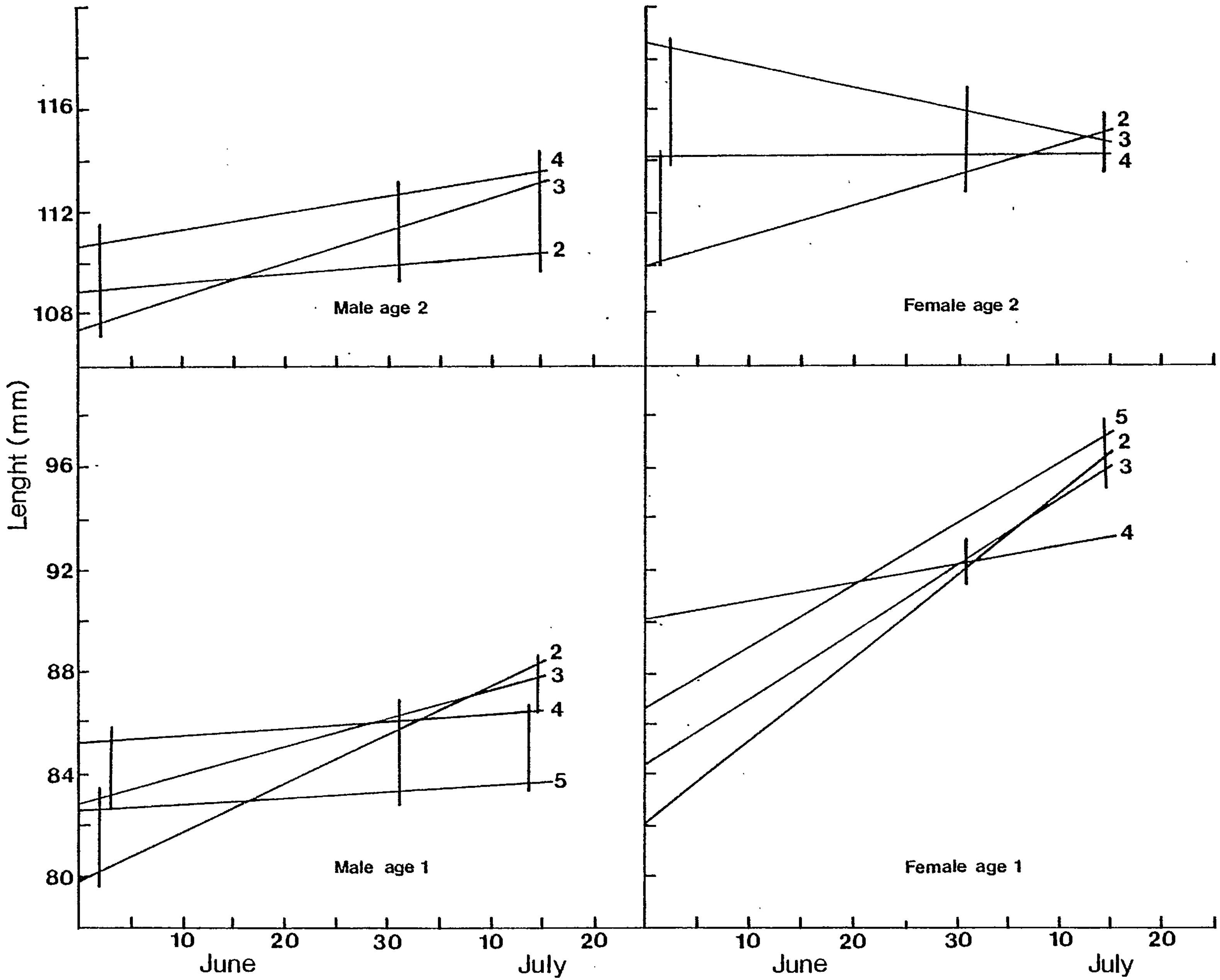

FIG. 5. Temporal changes, by site, in mean lengths of different age-sex groups of adult Atlantic silversides from the Annapolis River, 1980.

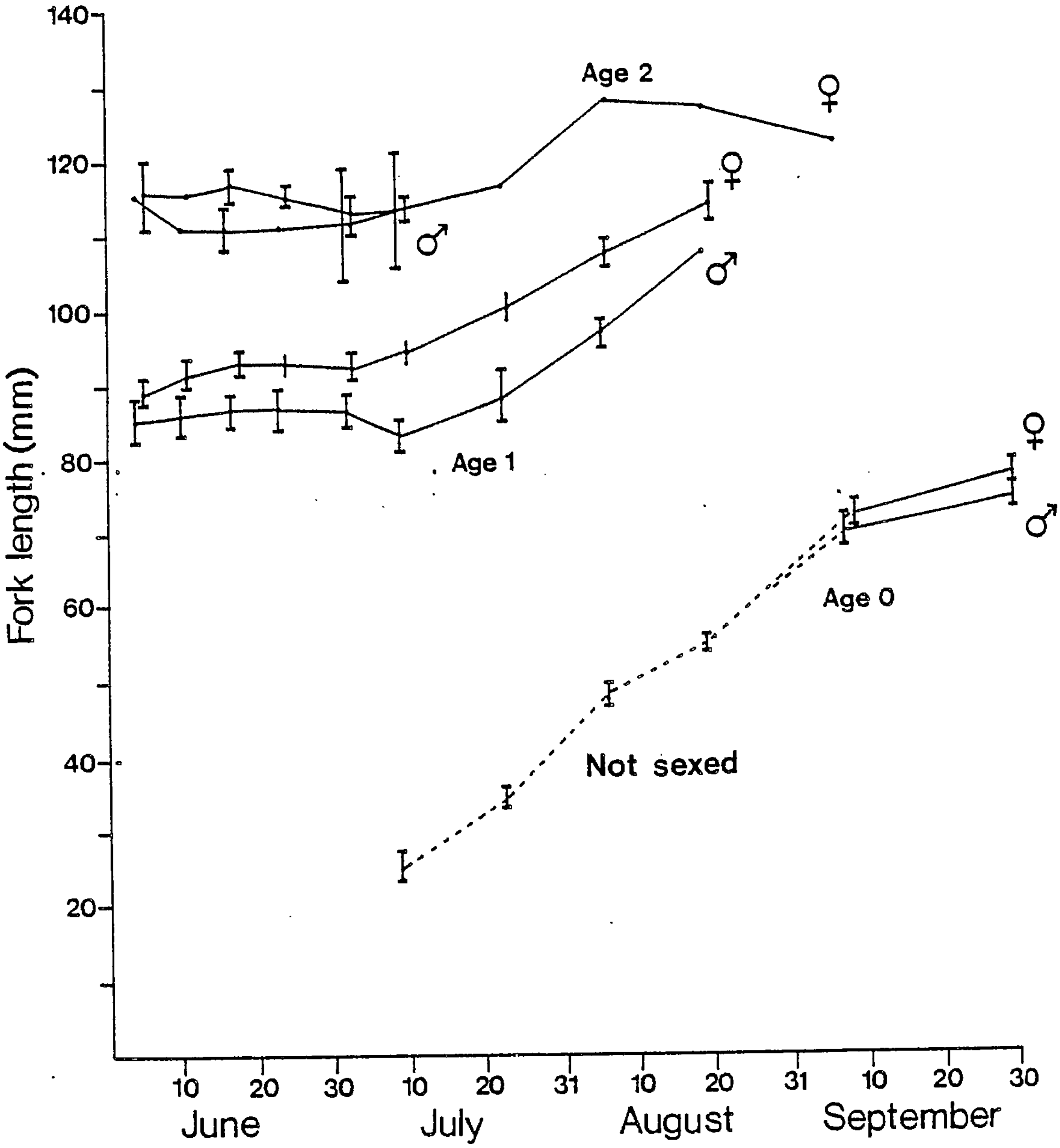

FIG. 6. Growth in length, by age-group, of Atlantic silversides from the Annapolis River, 1980.

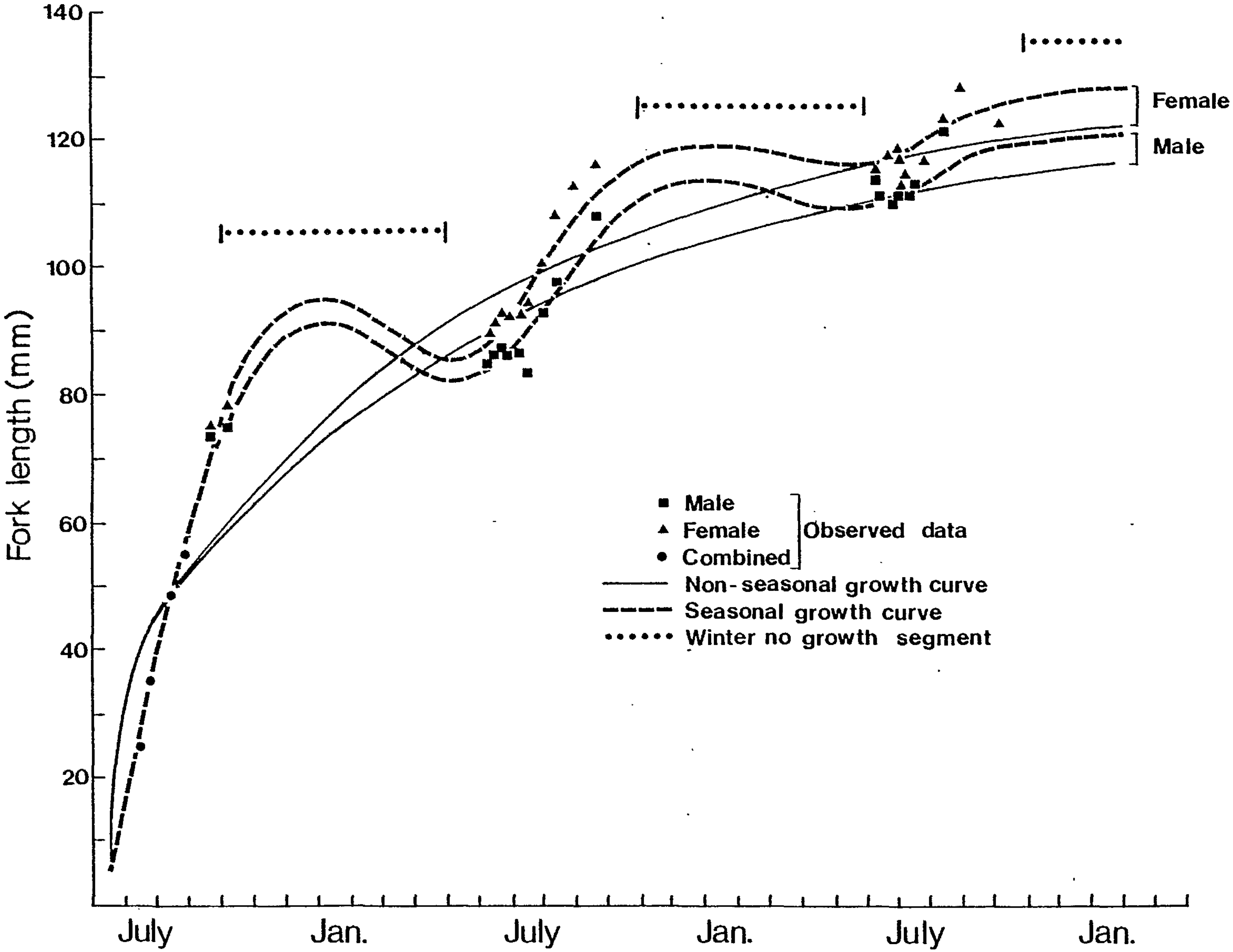

FIG. 7. Calculated annual and seasonal growth curves, based upon the 3-parameter von Bertalanffy growth function, for Atlantic silversides from the Annapolis River, 1980.

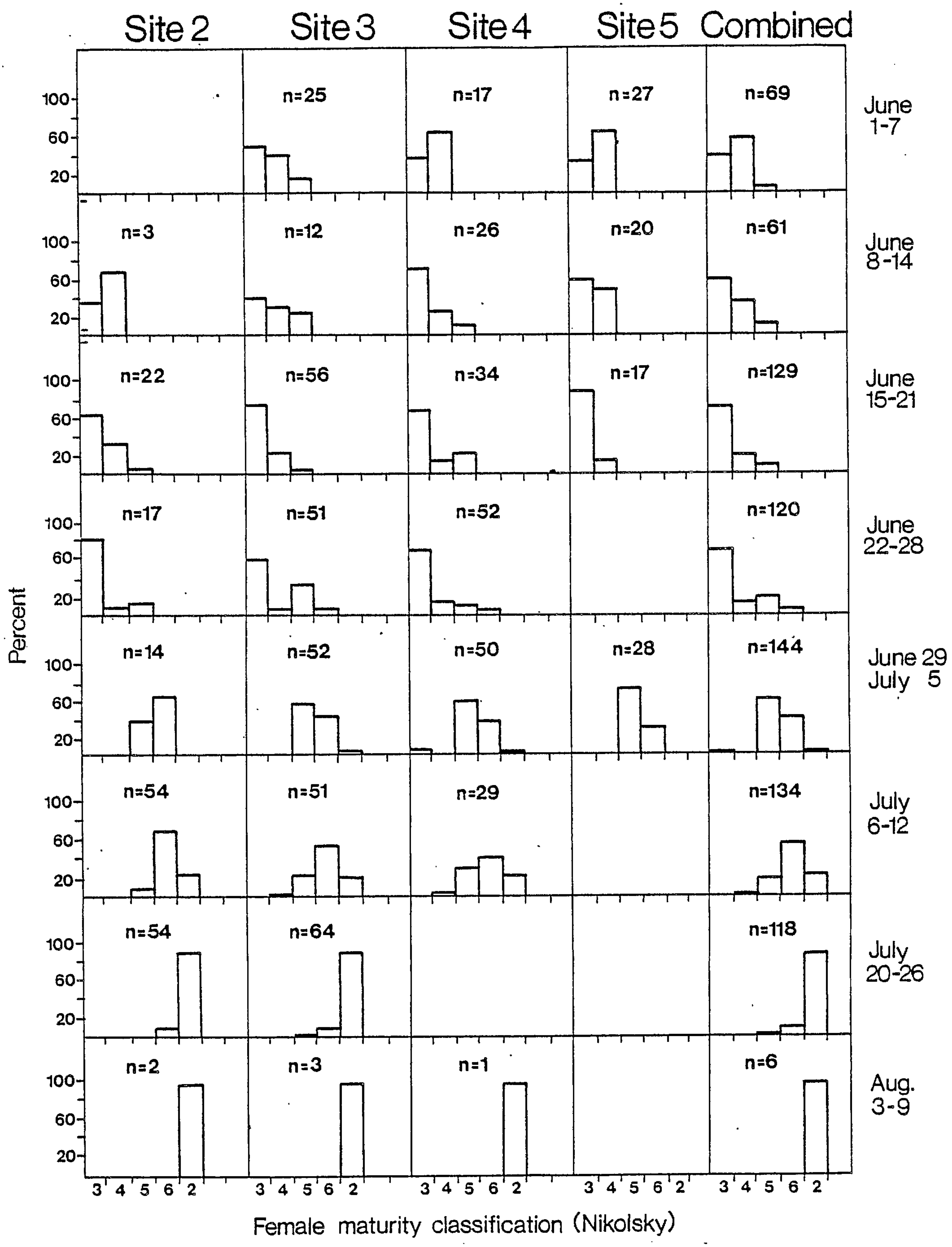

FIG. 8. Temporal changes, by site, in maturity classification for female Atlantic silversides from the Annapolis River, 1980.

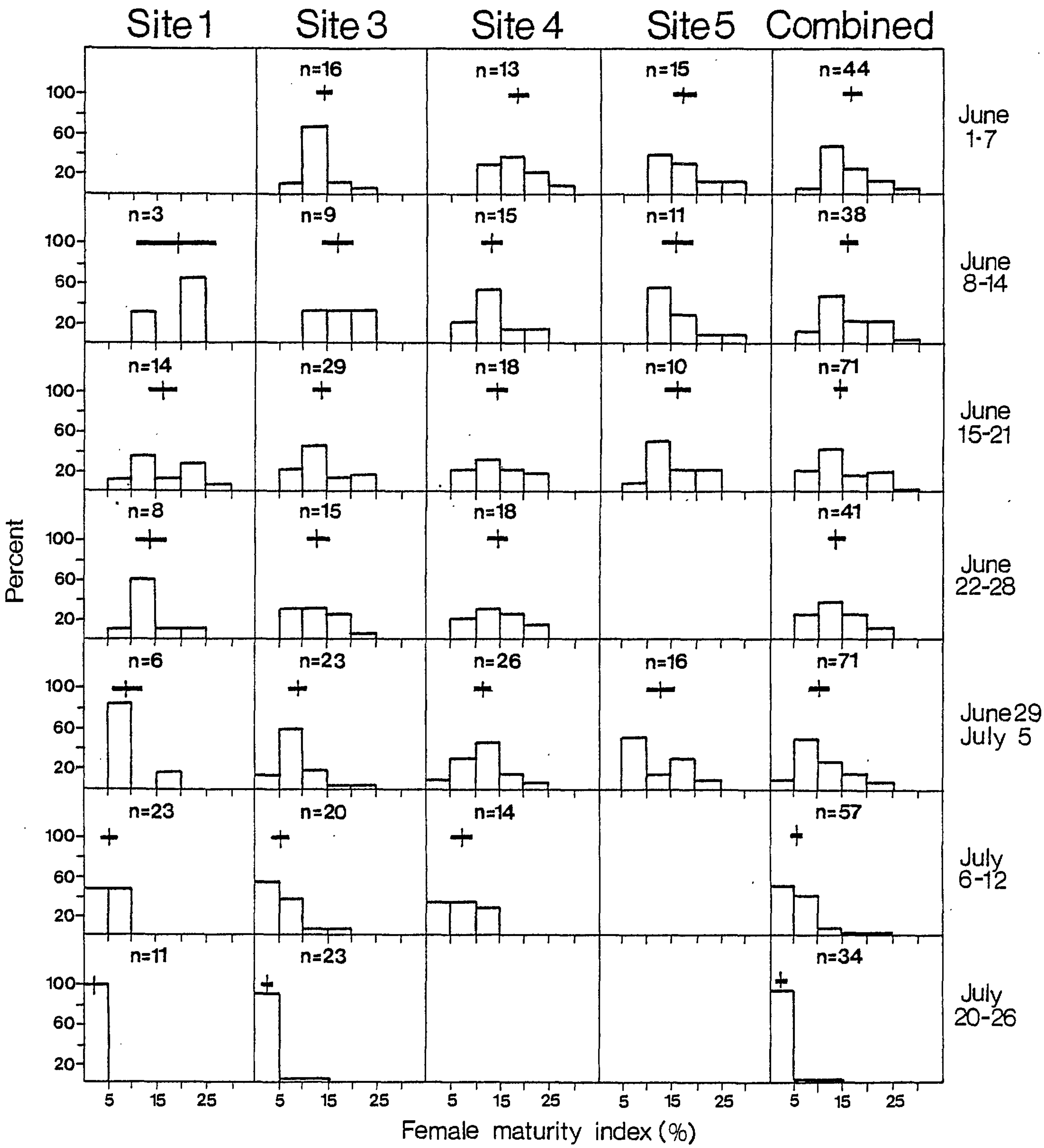

FIG. 9. Temporal changes, by site, in maturity index for female Atlantic silversides from the Annapolis River, 1980.

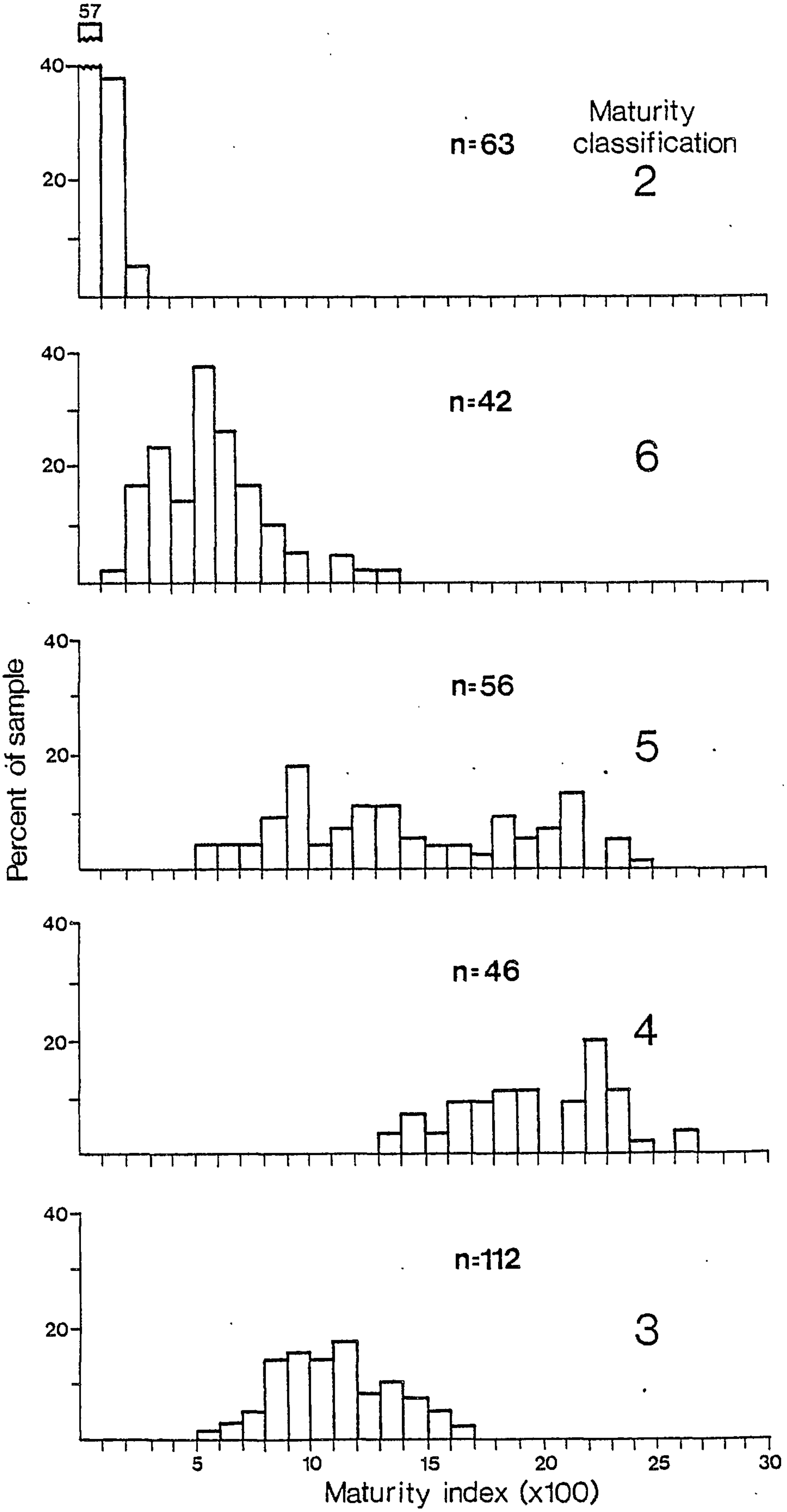

FIG. 10. Relationship between maturity classification and maturity index for female Atlantic silversides from the Annapolis River, 1980.

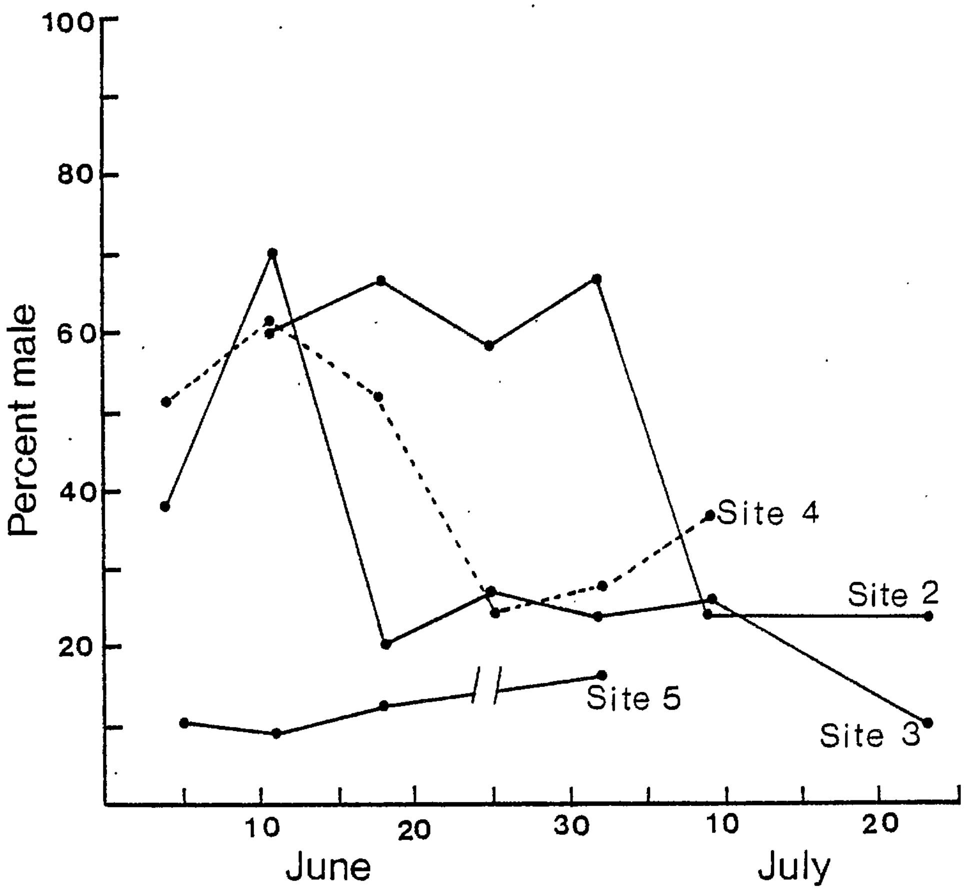

FIG. 11. Percentage, by site and week, of male Age-1 Atlantic silversides from the Annapolis River, 1980.

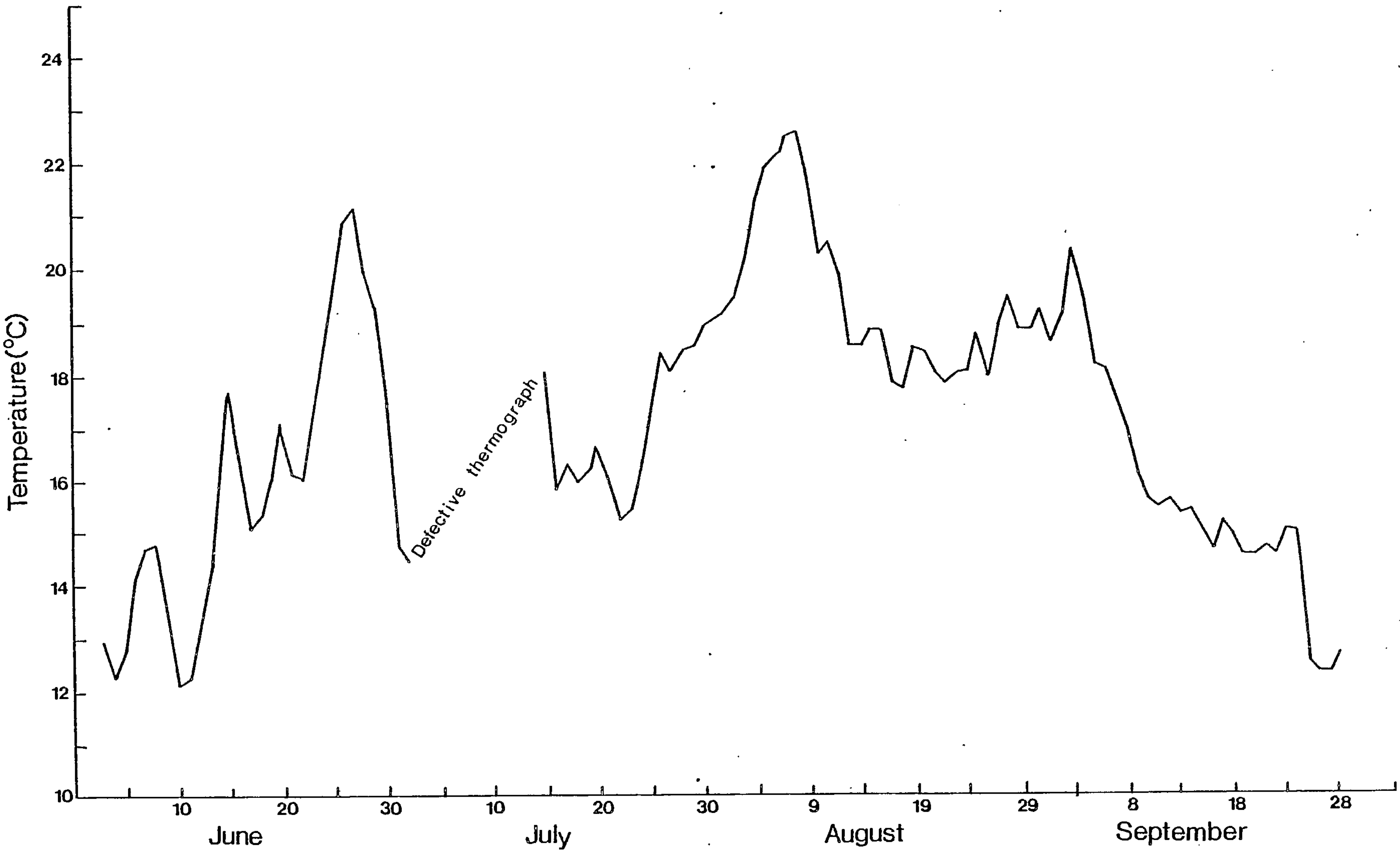

FIG. 12. Daily water temperatures at 1-m depth at Bridgetown, Annapolis River, 1980.

APPENDIX A

LENGTH (MM) COMPARISONS, BY SAMPLE DATE AND SEX, BETWEEN AGE-1 AND AGE-2 ATLANTIC SILVERSIDES IN THE ANNAPOLIS RIVER, 1980

	Male						Female					
	Age 1			Age 2			Age 1			Age 2		
Week	n	Min.	Max.	n	Min.	Max.	n	Min.	Max.	n	Min.	Max.
Site 1												
Jun 22-28	7	80	91	0	-	-	0	-	-	0	-	-
Aug 3-9	7	94	101	0	-	-	27	98	117	1	128	-
Aug 17-23	0	-	-	0	-	-	0	-	-	1	129	-
Sep 7-13	0	-	-	2	117	117	0	-	-	0	-	-
Site 2												
Jun 8-14	0	-	-	0	-	-	2	88	93	1	108	-
Jun 15-21	14	77	94	6	100	115	14	81	100	1	118	-
Jun 22-28	11	68	97	0	-	-	8	90	100	1	113	-
Jun 29-Jul 5	10	76	97	1	110	-	9	74	96	1	112	-
Jul 6-12	8	76	93	0	-	-	26	80	107	2	111	116
Jul 20-26	1	84	-	0	-	-	10	96	106	1	129	-
Aug 3-9	4	90	98	0	-	-	2	106	107	0	-	-
Sep 7-13	2	108	108	0	-	-	5	111	119	1	122	-
Sep 29	0	-	-	0	-	-	2	118	127	0	-	-
Site 3												
Jun 1-7	4	74	89	2	101	114	12	75	104	4	112	125
Jun 8-14	8	77	98	1	114	-	7	77	101	2	113	126
Jun 15-21	4	81	95	2	101	105	18	82	104	11	110	123
Jun 22-28	10	79	100	1	108	-	23	81	99	2	115	115
Jun 29-Jul 5	8	81	97	2	111	122	24	74	108	1	113	-
Jul 6-12	7	77	93	2	105	120	23	75	105	3	111	115
Jul 20-26	4	87	95	0	-	-	29	93	114	2	105	114[1]
Aug 3-9	2	96	104	0	-	-	2	103	108	1	118	-
Aug 19	0	-	-	0	-	-	5	107	118	0	-	-
Site 4												
Jun 1-7	11	73	97	2	115	116	19	81	103	1	112	-
Jun 8-14	19	68	96	1	108	-	15	80	106	0	-	-
Jun 15-21	14	72	96	3	111	118	15	78	104	4	109	123
Jun 22-28	5	76	93	1	113	-	29	85	103	1	117	-
Jun 29-Jul 5	8	72	94	1	103	-	25	78	103	2	111	118
Jul 6-12	8	76	92	2	109	120	14	87	108	3	110	117
Jul 20-26	0	-	-	0	-	-	0	-	-	0	-	-
Aug 3-9	7	91	103	0	-	-	1	103	-	0	-	-
Aug 17-23	0	-	-	0	-	-	0	-	-	0	-	-
Sep 7-13	0	-	-	1	122	-	0	-	-	0	-	-
Site 5												
Jun 1-7	5	82	87	0	-	-	29	64	102	0	-	-
Jun 8-14	0	-	-	0	-	-	11	86	101	0	-	-
Jun 15-21	0	-	-	0	-	-	10	88	102	0	-	-
Jun 22-28	0	-	-	0	-	-	0	-	-	0	-	-
Jun 29-Jul 5	1	79	-	0	-	-	15	91	100	1	109	-
Aug 29	0	-	-	0	-	-	0	-	-	1	127	-

[1]This is the only instance of overlap in length between different ages of a given sex.

APPENDIX B

NUMBERS OF ATLANTIC SILVERSIDES AGED BY SCALE AND ASSIGNED AGES, BY SITE AND AGE, ANNAPOLIS RIVER, 1980.

Site	Numbers of Atlantic silversides				
	Scale aged		Assigned age		
	Age 1	Age 2	Age 1	Age 2	Total
1	36	2	42	0	80
2	126	15	168	3	312
3	190	34	204	2	430
4	192	22	190	1	405
5	71	1	69	3	144
Total	615	74	673	9	1,371

APPENDIX C

NUMBERS OF ATLANTIC SILVERSIDES CAUGHT, BY SAMPLING DATE AND SITE, IN THE ANNAPOLIS RIVER, 1980.

Week	Site 1			Site 2			Site 3			Site 4			Site 5		
	No. of sweeps	Adult	Juv.	No. of sweeps	Adult	Juv.	No. of sweeps	Adult	Juv.	No. of sweeps	Adult	Juv.	No. of sweeps	Adult	Juv.
Jun 1–7		–		2	0		6	38		1	164		5	82	
Jun 8–14 [1]		–		4	6		2	2		5	77		4	22	
Jun 15–21		–		5	93		1	148		1	85		5	19	
Jun 22–28	4	7		4	40		1	74		5	83		4	1	
Jun 29–Jul 5	3	3		5	41		1	83		4	129		5	32	
Jul 6–12	3	2		1	112	*	1	110	*	5	46	*	4	0	*
Jul 20–26	4	0	*	1	209	*	2	98	*	4	0	*	2	0	*
Aug 3–9	1	120	130	2	6	188	2	5	1,300+	2	8	263	4	0	27
Aug 17–23	3	1	109	2	4	478	3	6	422	3	0	259	3	1	63
Sep 7–13	1	2	185	4	8	86	5	0	30	2	1	421	2	0	87
Sep 28–Oct 4	2	0	200	4	2	70	3	0	89	3	0	72	6	0	70
Mean	2.8	16.9	156.0	3.1	47.4	205.5	2.5	51.3	460+	3.2	53.9	253.8	4.0	14.3	61.8

[1]Difficult seining due to high winds and wave action.
*Abundant, uncounted larval and small silversides < ≈ 30 mm long.

APPENDIX D

SAMPLE STATISTICS, BY SITE AND WEEK, FOR ADULT (AGE-1 AND AGE-2) ATLANTIC SILVERSIDES FROM THE ANNAPOLIS RIVER, 1980

Week	n	Length (mm) Mean	SD	Range	Weight (g) Mean	SD	Range
Site 1							
Jun 1-7	0	-	-	-	-	-	-
Jun 8-14	0	-	-	-	-	-	-
Jun 15-21	0	-	-	-	-	-	-
Jun 22-28	7	86.7	5.47	80-96	4.57	1.303	3.47-7.10
Jun 29-Jul 5	3[1]	-	-	-	-	-	-
Jul 6-12	2[1]	-	-	-	-	-	-
Jul 20-26	0	-	-	-	-	-	-
Aug 3-9	70	106.4	5.98	94-128	7.91	1.215	5.45-10.80
Aug 17-23	1	129.0	-	-	14.35	-	-
Sep 7-13	2	117.0	-	117-117	11.95	-	11.03-12.86
Sep 29	0	-	-	-	-	-	-
Site 2							
Jun 1-7	0	-	-	-	-	-	-
Jun 8-14	6	91.3	9.99	77-108	5.93	2.301	2.91-9.90
Jun 15-21	70	89.3	9.86	71-118	5.60	1.824	2.62-14.00
Jun 22-28	39	87.2	8.71	68-113	5.09	1.521	2.36-8.60
Jun 29-Jul 5	42	86.6	9.39	66-112	4.67	1.504	2.28-9.30
Jul 6-12	70	91.8	8.17	72-116	5.51	1.377	2.79-9.62
Jul 20-26	70	99.1	7.89	84-127	6.46	1.406	3.84-10.35
Aug 3-9	6	99.0	6.45	90-107	6.60	1.535	4.82-9.04
Aug 17-23	0	-	-	-	-	-	-
Sep 7-13	8	114.5	5.10	108-122	10.38	1.745	8.07-13.65
Sep 29	2	122.5	-	118-127	12.30	-	11.05-13.55
Site 3							
Jun 1-7	38	89.2	13.08	68-125	5.68	2.426	2.48-12.02
Jun 8-14	36	89.6	11.03	77-126	5.75	2.367	3.18-13.50
Jun 15-21	70	95.1	12.70	71-123	7.16	2.820	3.02-14.40
Jun 22-28	70	89.1	7.60	74-115	5.58	1.399	3.26-11.14
Jun 29-Jul 5	70	91.7	8.40	74-122	5.78	1.369	3.20-10.36
Jul 6-12	70	91.8	8.91	74-120	5.74	1.586	3.03-10.80
Jul 20-26	70	99.3	6.12	86-114	6.90	1.220	4.40-10.97
Aug 3-9	5	105.8	8.08	96-118	8.08	1.991	6.16-11.11
Aug 17-23	5	112.6	5.23	107-118	9.55	1.680	7.43-11.49
Sep 7-13	0	-	-	-	-	-	-
Sep 29	0	-	-	-	-	-	-
Site 4							
Jun 1-7	70	90.2	8.62	73-116	5.93	1.636	2.99-11.44
Jun 8-14	70	87.7	7.31	68-108	5.19	1.352	2.28-9.77
Jun 15-21	70	91.5	10.74	72-123	6.11	1.995	3.07-13.15
Jun 22-28	70	90.0	7.86	70-117	5.78	1.609	2.56-12.20
Jun 29-Jul 5	70	89.9	8.32	72-118	5.85	1.647	3.13-12.23
Jul 6-12	46	93.4	10.32	76-120	6.55	2.033	3.49-12.67
Jul 20-26	0	-	-	-	-	-	-
Aug 3-9	8	95.6	4.69	91-103	6.13	0.755	5.21-7.44
Aug 17-23	0	-	-	-	-	-	-
Sep 7-13	1	122.0	-	-	12.21	-	-
Sep 29	0	-	-	-	-	-	-
Site 5							
Jun 1-7	70	87.5	8.91	64-111	5.67	1.648	2.10-10.17
Jun 8-14	22	88.8	6.78	74-101	5.89	1.287	3.23-9.57
Jun 15-21	19	92.0	5.56	79-102	6.31	1.154	3.47-8.33
Jun 22-28	0	-	-	-	-	-	-
Jun 29-Jul 5	33	92.5	6.53	79-109	6.24	1.228	3.70-8.07
Jul 6-12	0	-	-	-	-	-	-
Jul 20-26	0	-	-	-	-	-	-
Aug 3-9	0	-	-	-	-	-	-
Aug 17-23	1	127.0	-	-	13.70	-	-
Sep 7-13	0	-	-	-	-	-	-
Sep 29	0	-	-	-	-	-	-

[1]Data unrecorded.

APPENDIX E

SAMPLE STATISTICS, BY SITE AND WEEK, FOR ADULT (AGE-1) ATLANTIC SILVERSIDES FROM THE ANNAPOLIS RIVER, 1980

Week	n	Length (mm) Mean	SD	Range	Weight (g) Mean	SD	Range
Site 1							
Jun 1-7	0	-	-	-	-	-	-
Jun 8-14	0	-	-	-	-	-	-
Jun 15-21	0	-	-	-	-	-	-
Jun 22-28	7	86.7	5.47	80-96	4.57	1.303	3.47-7.10
Jun 29-Jul 5	3[1]	-	-	-	-	-	-
Jul 6-12	2[1]	-	-	-	-	-	-
Jul 20-26	0	-	-	-	-	-	-
Aug 3-9	69	106.1	5.42	94-117	7.86	1.160	5.45-9.97
Aug 17-23	0	-	-	-	-	-	-
Sep 7-13	2	117.0	-	117-117	11.95	-	11.03-12.86
Sep 29	0	-	-	-	-	-	-
Site 2							
Jun 1-7	0	-	-	-	-	-	-
Jun 8-14	5	88.0	6.44	77-93	5.14	1.378	2.91-6.53
Jun 15-21	63	87.0	6.86	71-100	5.24	1.349	2.62-8.84
Jun 22-28	38	86.5	7.71	68-100	5.01	1.438	2.36-8.60
Jun 29-Jul 5	39	85.4	7.75	66-97	4.51	1.248	2.28-6.66
Jul 6-12	68	91.1	7.35	72-107	5.39	1.223	2.79-8.37
Jul 20-26	66	98.0	6.28	84-110	6.26	1.163	3.84-9.08
Aug 3-9	6	99.0	6.45	90-107	6.60	1.535	4.82-9.04
Aug 17-23	0	-	-	-	-	-	-
Sep 7-13	7	113.4	4.43	108-119	9.91	1.231	8.07-11.51
Sep 29	2	122.5	-	118-127	12.30	-	11.05-13.55
Site 3							
Jun 1-7	34	85.9	9.24	68-104	5.02	1.526	2.48-9.05
Jun 8-14	33	87.0	7.00	77-101	5.20	1.495	3.18-8.98
Jun 15-21	56	90.0	7.72	71-107	6.02	1.649	3.02-9.74
Jun 22-28	67	88.1	5.79	74-100	5.39	1.033	3.26-7.66
Jun 29-Jul 5	67	90.7	6.80	74-108	5.64	1.194	3.20-9.00
Jul 6-12	65	90.2	6.88	74-102	5.46	1.217	3.03-8.25
Jul 20-26	63	98.3	5.42	86-114	6.72	1.068	4.40-9.40
Aug 3-9	4	102.8	4.99	96-108	7.32	1.208	6.16-9.02
Aug 17-23	5	112.6	5.23	107-118	9.55	1.680	7.43-11.49
Sep 7-13	0	-	-	-	-	-	-
Sep 29	0	-	-	-	-	-	-
Site 4							
Jun 1-7	67	89.0	7.06	73-105	5.69	1.301	2.99-9.16
Jun 8-14	69	87.5	6.52	68-108	5.15	1.183	2.28-9.77
Jun 15-21	62	88.7	7.48	72-104	5.58	1.302	3.07-9.09
Jun 22-28	68	89.3	6.71	70-103	5.64	1.379	2.56-9.23
Jun 29-Jul 5	67	89.0	7.08	72-104	5.63	1.271	3.13-8.36
Jul 6-12	41	90.9	7.62	76-108	6.04	1.405	3.49-9.63
Jul 20-26	0	-	-	-	-	-	-
Aug 3-9	8	95.6	4.69	91-103	6.13	0.755	5.21-7.44
Aug 17-23	0	-	-	-	-	-	-
Sep 7-13	0	-	-	-	-	-	-
Sep 29	0	-	-	-	-	-	-
Site 5							
Jun 1-7	67	86.6	7.76	64-102	5.51	1.447	2.10-8.69
Jun 8-14	22	88.8	6.78	74-101	5.89	1.287	3.23-9.57
Jun 15-21	19	92.0	5.56	79-102	6.31	1.154	3.47-8.33
Jun 22-28	0	-	-	-	-	-	-
Jun 29-Jul 5	32	92.0	5.92	79-100	6.17	1.202	3.70-8.07
Jul 6-12	0	-	-	-	-	-	-
Jul 20-26	0	-	-	-	-	-	-
Aug 3-9	0	-	-	-	-	-	-
Aug 17-23	0	-	-	-	-	-	-
Sep 7-13	0	-	-	-	-	-	-
Sep 29	0	-	-	-	-	-	-

[1] Data unrecorded.

APPENDIX F

SAMPLE STATISTICS, BY SITE AND WEEK, FOR ADULT (AGE-2) ATLANTIC SILVERSIDES FROM THE ANNAPOLIS RIVER, 1980[1]

		Length (mm)			Weight (g)		
Week	n	Mean	SD	Range	Mean	SD	Range
Site 2							
Jun 1-7	0	-	-	-	-	-	-
Jun 8-14	1	108.0	-	-	9.90	-	-
Jun 15-21	7	110.7	6.37	100-118	8.85	2.413	6.44-14.00
Jun 22-28	1	113.0	-	-	8.41	-	-
Jun 29-Jul 5	2	111.0	-	110-112	8.46	-	7.61-9.30
Jul 6-12	2	113.5	-	111-116	9.36	-	9.09-9.62
Jul 20-26	4	118.3	7.68	114-127	9.74	0.944	9.76-10.35
Aug 3-9	0	-	-	-	-	-	-
Aug 17-23	0	-	-	-	-	-	-
Sep 7-13	1	122.0	-	-	13.65	-	-
Sep 29	0	-	-	-	-	-	-
Site 3							
Jun 1-7	4	116.8	6.19	112-125	11.27	0.595	10.66-12.02
Jun 8-14	3	117.7	7.23	113-126	11.79	1.591	10.35-13.50
Jun 15-21	14	115.7	5.66	106-123	11.71	1.688	9.16-14.40
Jun 22-28	3	112.7	4.04	108-115	9.89	1.792	7.84-11.14
Jun 29-Jul 5	3	115.3	5.86	111-122	8.97	1.294	7.80-10.36
Jul 6-12	5	112.6	5.51	105-120	9.36	1.425	7.22-10.80
Jul 20-26	3	110.7	4.93	105-114	9.59	1.320	8.34-10.97
Aug 3-9	1	118.0	-	-	11.11	-	-
Aug 17-23	0	-	-	-	-	-	-
Sep 7-13	0	-	-	-	-	-	-
Sep 29	0	-	-	-	-	-	-
Site 4							
Jun 1-7	3	114.3	2.08	112-116	10.51	0.826	9.86-11.44
Jun 8-14	1	108.0	-	-	8.43	-	-
Jun 15-21	8	113.5	4.93	108-123	10.23	1.610	8.00-13.15
Jun 22-28	2	114.5	-	112-117	10.47	-	8.73-12.20
Jun 29-Jul 5	3	110.7	7.51	103-118	10.77	1.502	9.23-12.23
Jul 6-12	5	114.0	4.64	109-120	10.74	1.467	9.14-12.67
Jul 20-26	0	-	-	-	-	-	-
Aug 3-9	0	-	-	-	-	-	-
Aug 17-23	0	-	-	-	-	-	-
Sep 7-13	1	122.0	-	-	12.21	-	-
Sep 29	0	-	-	-	-	-	-
Site 5							
Jun 1-7	3	109.3	2.08	107-111	9.56	0.522	9.10-10.17
Jun 8-14	0	-	-	-	-	-	-
Jun 15-21	0	-	-	-	-	-	-
Jun 22-28	0	-	-	-	-	-	-
Jun 29-Jul 5	1	109.0	-	-	8.07	-	-
Jul 6-12	0	-	-	-	-	-	-
Jul 20-26	0	-	-	-	-	-	-
Aug 3-9	0	-	-	-	-	-	-
Aug 17-23	1	127.0	-	-	13.07	-	-
Sep 7-13	0	-	-	-	-	-	-
Sep 29	0	-	-	-	-	-	-

[1]Two Age-2 fish were captured at Site 1: August 6, 128 mm, 10.80 g; August 19, 129 mm, 14.35 g.

APPENDIX G

SAMPLE STATISTICS, BY SITE AND WEEK, FOR JUVENILE (AGE-0) ATLANTIC SILVERSIDES FROM THE ANNAPOLIS RIVER, 1980

Week	n	Length (mm)			Weight (g)		
		Mean	SD	Range	Mean	SD	Range
Site 1							
Jul 6-12	0[1]	-	-	-	-	-	-
Jul 20-26	70	33.0	4.54	22-44	0.26	0.102	0.04-0.58
Aug 3-9	70	57.5	6.43	39-72	1.30	0.390	0.44-2.31
Aug 17-23	70	55.1	10.32	38-76	1.10	0.605	0.36-2.60
Sep 7-13	70	63.7	9.33	42-87	1.67	0.816	0.54-4.03
Sep 29	70	54.6	14.21	40-86	1.21	0.994	0.41-3.86
Site 2							
Jul 6-12	0[1]	-	-	-	-	-	-
Jul 20-26	70	37.0	7.43	16-54	0.41	0.209	0.03-1.14
Aug 3-9	70	43.3	9.89	26-66	0.65	0.413	0.14-1.92
Aug 17-23	69	62.5	13.00	38-83	1.62	0.880	0.33-3.46
Sep 7-13	70	71.0	18.10	37-96	2.63	1.680	0.30-5.92
Sep 29	70	82.9	13.28	45-103	3.91	1.796	0.52-7.76
Site 3							
Jul 6-12	0[1]	-	-	-	-	-	-
Jul 20-26	64	39.8	7.54	17-54	0.51	0.256	0.03-1.18
Aug 3-9	70	47.9	11.82	24-68	0.97	0.562	0.10-2.30
Aug 17-23	70	57.8	10.43	36-82	1.37	0.725	0.37-3.42
Sep 7-13	30	54.5	13.50	34-81	1.17	0.910	0.27-3.78
Sep 29	70	67.6	9.71	41-97	1.95	0.913	0.43-6.12
Site 4							
Jul 6-12	34	23.4	6.26	12-36	0.11	0.777	0.10-0.24
Jul 20-26	70	30.4	10.22	12-50	0.27	0.243	0.10-0.88
Aug 3-9	71	48.0	7.62	32-65	0.89	0.382	0.28-1.91
Aug 17-23	70	47.8	6.34	36-72	0.78	0.315	0.36-2.40
Sep 7-13	70	60.6	9.88	25-82	1.62	0.702	0.12-3.91
Sep 29	70	75.9	13.57	34-99	3.04	1.499	0.26-6.46
Site 5							
Jul 6-12	28	27.3	4.72	13-33	0.17	0.073	0.10-0.29
Jul 20-26	24	30.0	10.37	14-45	0.25	0.212	0.10-0.63
Aug 3-9	28	43.2	8.79	20-56	0.67	0.341	0.55-1.29
Aug 17-23	65	51.8	14.09	30-76	1.17	0.861	0.19-3.32
Sep 7-13	70	65.4	10.12	42-90	2.04	0.962	0.54-4.75
Sep 29	69	70.4	6.76	40-86	2.23	0.591	0.44-4.10

[1]Young fish abundant but too small for effective sampling.

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