

1980

The Growth and Life-History Strategy of the Soft-Shell Clam, *Mya arenaria L.*

Richard S. Appeldoorn
University of Rhode Island

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THE GROWTH AND LIFE-HISTORY STRATEGY OF THE
SOFT-SHELL CLAM, Mya arenaria L.

BY

DOCTOR OF PHILOSOPHY
RICHARD S. APPELDOORN

RICHARD S. APPELDOORN

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

IN

Approved:

OCEANOGRAPHY

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UNIVERSITY OF RHODE ISLAND
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1980

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ABSTRACT

The growth and life-history strategy of the soft-shell clam, Mya arenaria were analyzed through the examination of 25 populations spread throughout the species' geographic range. Growth rate was determined by length-frequency analysis and was analyzed using Gallucci and Quinn's w parameter of the von Bertalanffy equation. Principal components analysis (PCA) was used to analyze environmental variability. Variations in growth were related to environmental differences. Growth varied inversely with latitude. This relationship was due mostly to temperature differences. PCA indicated that several environmental factors varied systematically with latitude. Growth was found to be negatively correlated to the siltiness of the sediment and to the concentration of sedimentary hydrocarbons. Distinct shifts in growth rate occurred when environmental quality was significantly altered by a discrete pollution event. Growth was reduced in response to heavy metal effluents and oil spills. Fairly rapid recovery followed heavy metal pollution abatement. Recovery at oil spill sites was variable but slow.

The relationships between various life-history parameters were analyzed to elucidate the species' modes of adaptation and life-history strategy. Within the context of latitudinal variations in the environment an association was found between decreasing latitude and: faster growth, greater variation in juvenile mortality, larger maturation size, larger egg size, lower egg density and decreasing longevity. These relationships indicated that M. arenaria follows a bet-hedging life-history strategy. On a local scale a

positive relationship was found between larger egg size and greater egg density. This trend appeared to be associated with the condition of the population and may represent a physiological response to local environmental conditions.

The proportion of females (52%) was found to be significantly greater than the proportion of males. No evidence of a mechanism behind this disparity was detected.

The study as a whole contributes to our understanding of the life history of *Mya arenaria* in the environment. No limitations were encountered. First, because the analysis was designed after data collection many of the assumptions in the analysis were not strictly valid for their application in this study. The greatest limitation was insufficient data on the most variability in the population. These variables could have been added at the time of sampling. Second, in attempt to make the inferences and support conclusions based on the data was made through further sampling or experimentation. Although such work would be a welcome addition, it is believed that this work would contribute to the study with itself. It is felt that the present analysis was done by itself with the questions remaining to be answered serving as an incentive for further study.

PREFACE

This thesis was prepared according to manuscript format. Three manuscripts are presented and each is written in a style appropriate for submission to a particular scientific journal. The first manuscript will be submitted to *Marine Biology*; the second manuscript has been submitted to the *Proceedings of the National Shellfisheries Association*; and the third manuscript will be submitted to *Oecologia*.

The thesis as a whole constitutes an analysis of data collected during a study of neoplasia in *Mya arenaria* and pollution in the environment. Two limitations were encountered. First, because the analysis was designed after data collection many of the measurements in the raw data were not entirely suited for their application in this study. The problems included no or insufficient data and too much variability in the measurements. These problems could have been solved at the time of sampling. Second, no attempt was made to investigate and support conclusions based on the data analysis through further sampling or experimentation. Although such work would be a welcome addition, it is believed that this work would constitute a thesis unto itself. It is felt that the present analysis can stand by itself with the questions remaining to be answered serving as an incentive for further study.

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Many people, at various levels and degrees, were involved in this study. Special thanks go to Saul Saila, my major professor, who provided financial support for data collection and analysis (through a grant from the American Petroleum Institute), and who provided helpful ideas, moral support, and valuable criticism throughout my graduate tenure. Equal thanks go to my parents and to M. Schwanke for their loving moral support and critical financial support during leaner times. Drs. R.C. Bullock and A.N. Sastry gave helpful suggestions for the thesis and provided valued commentary on graduate education in general. Many people were involved in data collection. I would particularly like to acknowledge the assistance of R.L. Dow, M. Richards, J.M. Hickey, M.L.H. Thomas, and M. Worobec in clam collection. R.S. Brown, J. Keller, A. Miller, S. Polofsky, and others at Peckham Farm were responsible for much of the sample processing and data compilation. Several people, particularly H. Walker, helped soothe my statistical nightmares, real or imagined. C. Brown and E. Franklin provided the hydrocarbon analyses used in this study. Technical assistance in analysis and manuscript preparation was provided by Drs. R.L. MacMaster, T.A. Napora, and R.E. Wolke. I am grateful to my friends for having put up with me and my sense of humor (real or imagined?) and for providing valued companionship.

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ABSTRACT

The growth rate of the soft-shell clam, Mya arenaria, was estimated for 25 populations using length-frequency analysis. Variations in the growth rate between local stocks were related to differences in the environment. The analysis of growth was based on

VARIATION IN THE GROWTH RATE OF Mya arenaria AND ITS RELATIONSHIP TO THE ENVIRONMENT AS ANALYZED THROUGH PRINCIPAL COMPONENTS ANALYSIS AND THE ω PARAMETER OF THE VON BERTALANFFY EQUATION

analysis. This analysis yielded three environmental factors: salinity, siltiness, and sedimentary hydrocarbons. Growth was found to be significantly related to each of the above components. A distinct latitudinal growth relationship was observed with growth decreasing towards the north. Analysis of the first component, salinity, showed that many environmental factors (temperature, tidal height, tidal position, adaptive conditions) systematically varied with salinity. The analysis indicated that temperature was the dominant factor responsible for the latitudinal trend in growth. Growth was negatively related to both siltiness and sedimentary hydrocarbons.

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analysis and the ω parameter of the von Bertalanffy equation. The analysis of growth was based on length-frequency analysis and the ω parameter of the von Bertalanffy equation. This analysis yielded three environmental factors: salinity, siltiness, and sedimentary hydrocarbons. Growth was found to be significantly related to each of the above components. A distinct latitudinal growth relationship was observed with growth decreasing towards the north. Analysis of the first component, salinity, showed that many environmental factors (temperature, tidal height, tidal position, adaptive conditions) systematically varied with salinity. The analysis indicated that temperature was the dominant factor responsible for the latitudinal trend in growth. Growth was negatively related to both siltiness and sedimentary hydrocarbons.

ABSTRACT

The growth rate of the soft-shell clam, Mya arenaria, was estimated for 25 populations using length-frequency analysis. Variations in the growth rate between populations were related to differences in the environment. The analysis of growth was based on Gallucci and Quinn's ω parameter for the von Bertalanffy equation. Environmental variability was analyzed using principal component analysis. This analysis yielded three environmental factors: northness, siltiness, and sedimentary hydrocarbons. Growth was found to be significantly related to each of the three components. A distinct latitudinal growth relationship was observed with growth decreasing towards the north. Analysis of the first component, northness, showed that many environmental factors (temperature, tidal height, tidal position, edaphic conditions) systematically varied with latitude. The analysis indicated that temperature was the dominant factor responsible for the latitudinal trend in growth. Growth was negatively related to both siltiness and sedimentary hydrocarbons. Both principal component analysis and the parameter ω proved to be useful for the detailed study of environmental variability and growth variations respectively.

INTRODUCTION

The growth of Mya arenaria, the soft-shell clam, has been studied by many investigators (Wilton and Wilton, 1929; Belding, 1930; Newcombe, 1936; Swan, 1952; Brouseau, 1979; and others) and much work has been done in assessing the importance of various environmental factors to the growth process. These factors include water current and quality, food, temperature, salinity, various edaphic parameters, and pollution. In the past, investigators were obliged to study these factors individually even though it was realized that many were interrelated (Belding, 1930). Researchers often disagreed on the relative importance of each of these factors. With the advent of high-speed computers and the development of more sophisticated analytical techniques it is now possible to efficiently analyze complex ecological systems involving multiple factors.

The purpose of this study was to investigate the factors contributing to variations in the growth rate of soft clam populations. Principal components analysis was chosen for the multivariate analysis of the environmental data and the von Bertalanffy model was chosen for the analysis of growth using the recently introduced growth parameter ω of Gallucci and Quinn (1979). This study represents one of the first applications of ω for the investigation of growth variations. Of specific interest was a methodology which could establish the presence or absence of a latitudinal trend in growth and the factors responsible for it, since a definite relationship had yet to be demonstrated (Brouseau, 1979).

MATERIALS AND METHODS

The growth of Mya arenaria was studied at 25 sites located along the east coast of North America from Maryland to Nova Scotia (Figure 1). The sites were initially chosen and sampled as part of a study investigating the relationship between environmental pollution and neoplasia in Mya arenaria (Brown et al., 1979) and as such they varied greatly in their environmental quality. Estimates of the following environmental parameters were obtained for each site: salinity, tidal position, tidal range, average annual temperature, sedimentary grain size, dispersion and skewness of grain sizes, percent silt-clay, percent organic matter, and total sedimentary hydrocarbons.

Salinity, at low tide, was measured using a refractometer; tidal position was estimated on a scale of 0-1 where 0 = subtidal (never exposed) and 1 = full exposure (never submerged). Estimates of the average annual temperature at each site were obtained from various literature sources; estimates of the tidal range were obtained from the National Ocean Survey (1978).

Sediment samples were collected and analyzed to determine the amount of organic matter and the grain size distribution. Each sample consisted of a composite of two surface cores (21 cm² x 8 cm depth) which were kept frozen prior to analysis. Using a 74 μ m mesh screen an aliquot of the sediment sample was wet sieved to separate the sand fraction from the silt-clay fraction (Buchanann, 1971). The sand fraction was further analyzed by dry sieving (ASTM, 1962) using 7 screens (ranging from 4-0.062 mm mesh) set at one phi (ϕ) intervals. The phi scale is a log function of the millimeter

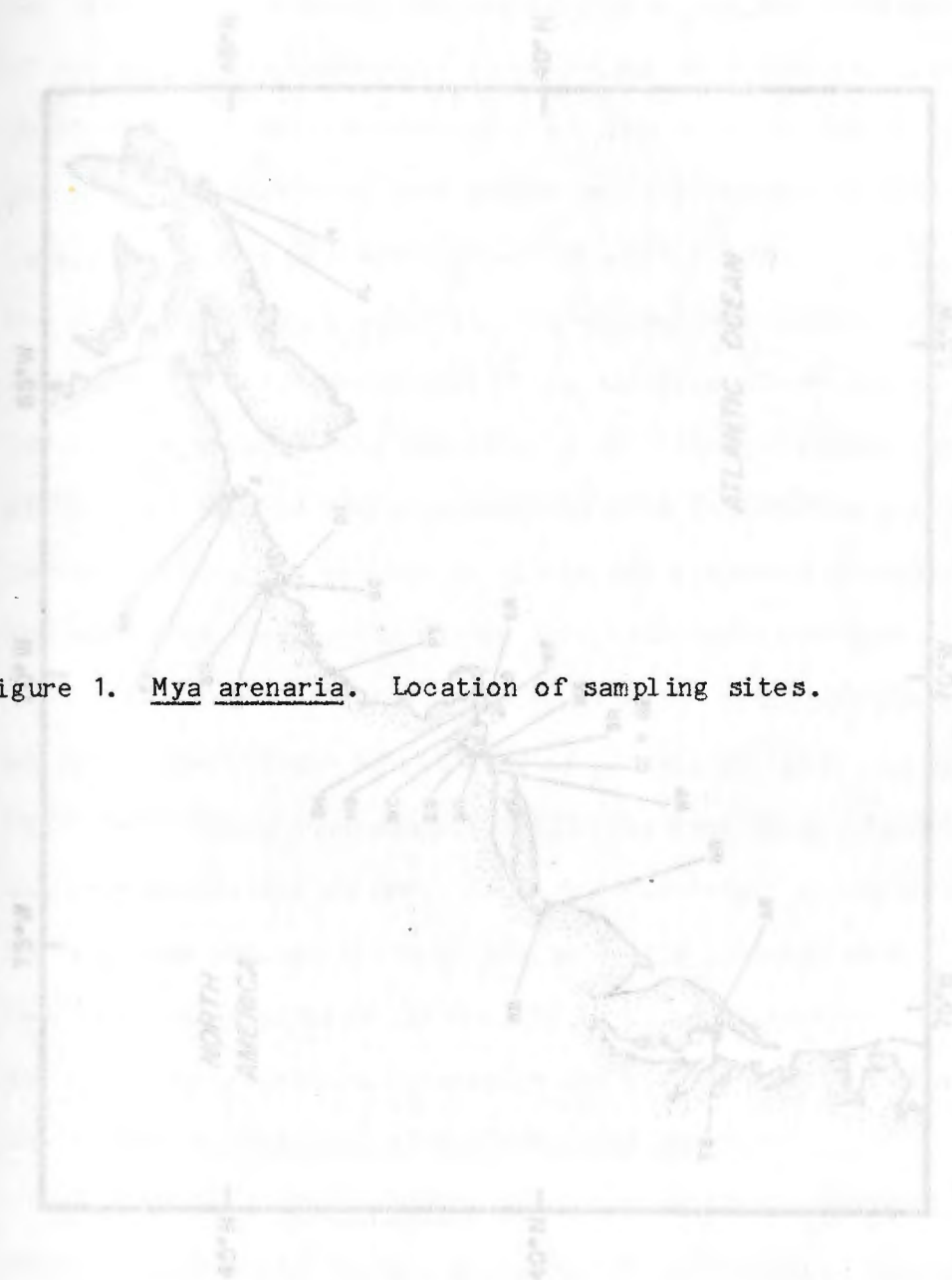
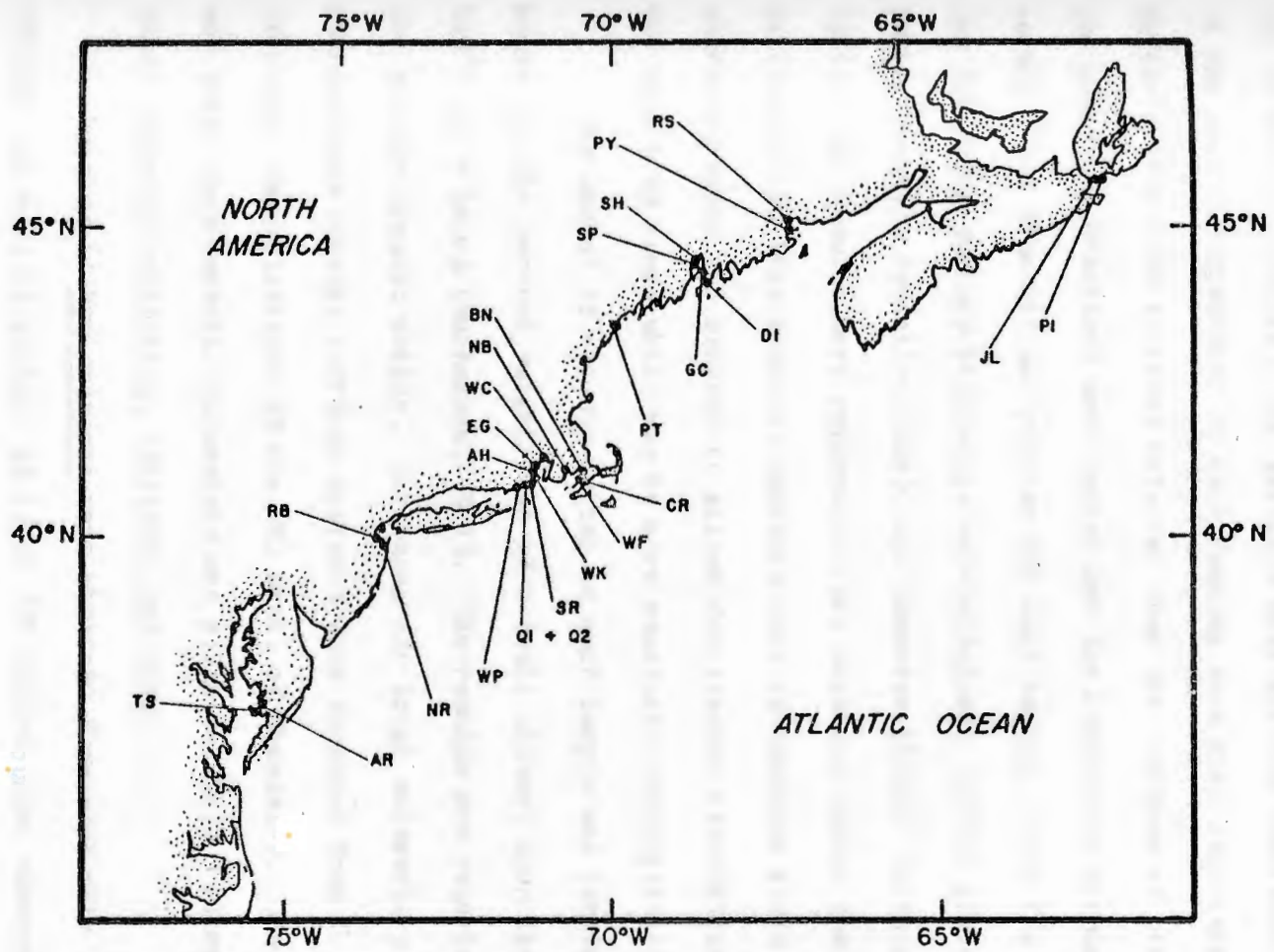


Figure 1. Mya arenaria. Location of sampling sites.



scale where $\phi = -\log_2(\text{mm})$. The silt-clay fraction was analyzed using the hydrometer method (ASTM, 1962) with readings taken at 2, 15, 60 and 120 minutes. The particle size and the cumulative percent of the sample represented at each reading were then calculated. The particle size distributions obtained from the analyses of the sand and silt-clay fractions were pooled and the cumulative frequency versus grain size (ϕ) was plotted for each sample. From the graphs the following summary statistics were obtained: median grain size ($Md\phi$), quartile deviation ($QD\phi$), and skewness ($Skq\phi$) (Buchanann, 1971). The results were reported in phi notation rather than in millimeters as this scale is commonly used to describe grain size characteristics and because it allows for greater discrimination in the silt-clay range which may be more meaningful biologically.

The amount of organic matter in each sample was determined by measuring the percent weight loss of a small aliquot upon ignition at 550°C for 4 hours (Buchanann, 1971). The results are reported as the percent organic matter. Estimates for total sedimentary hydrocarbons through infrared analysis were obtained from C. Brown (personal communication) of the URI Dept. of Chemistry. The sites and their environmental parameters are given in Table 1 along with their dates of collection, latitude, and code.

Samples of Mya arenaria were obtained from each site. An attempt was made to collect at least 180 individuals, however, this was not accomplished on all occasions. For each individual, shell length (maximum shell dimension) was measured to the nearest millimeter using vernier calipers. This information was used to determine the age structure of each population via length-frequency

Table 1. Sampling sites and their environmental parameters. -: missing value

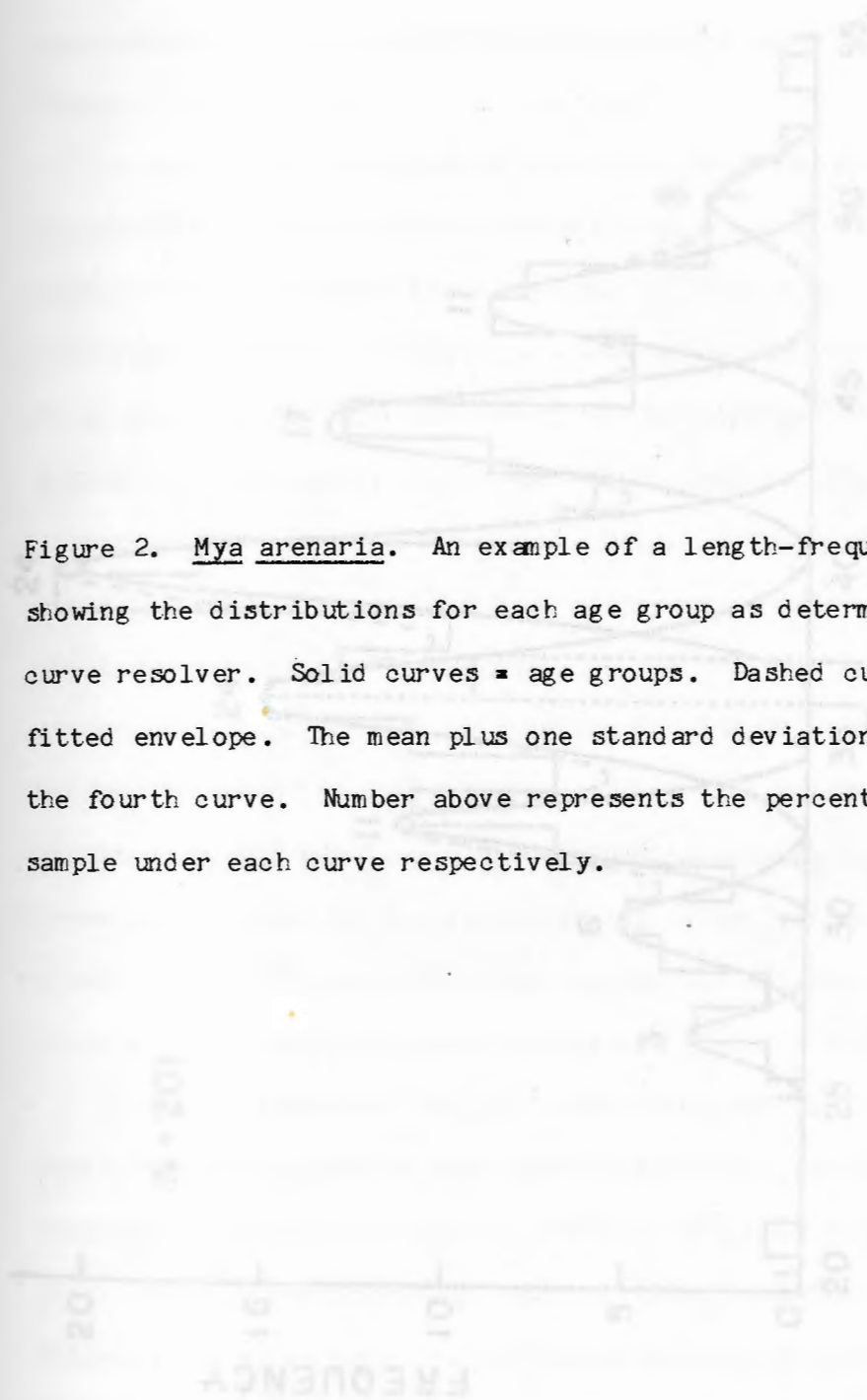
Sampling Site	Site Code	Date of Sampling	Latitude (°N)	Ave. Annual Temp.	Tidal Range ft (m)	Tidal Position	Mdφ	QDφ	Skqφ	% Silt-Clay	% Organ. Matter	Total Sedi. Hydro. (µg/g)	Salin. (ppt)
Tangier Sound MD	TS	27- 3-78	37.952	15.0 ^a	2.5 (0.77)	0	-	-	-	-	-	-	11
Big Annessex River MD	AR	27- 3-78	38.051	15.0 ^a	2.5 (0.77)	0	-	-	-	-	-	-	11
Navesink River NJ	NR	2- 6-77	40.377	13.0 ^b	3.5 (1.08)	.50	1.80	0.40	-0.10	1.0	1.5	114	24
Raritan Bay NJ	RB	1- 6-77	40.459	13.0 ^b	6.0 (1.85)	.50	2.55	0.44	-0.05	4.2	2.6	104	24
Winnapaug Pond RI	WP	18- 7-77	41.327	12.3 ^c	2.0 (0.62)	.50	1.97	0.62	0.01	1.5	0.7	21	31
Quonochontaug Pond-1 RI	Q1	22- 6-76	41.333	12.3 ^c	2.0 (0.62)	.35	1.00	0.60	0.00	0.7	1.5	0	31
Quonochontaug Pond-2 RI	Q2	4- 4-77	41.333	12.3 ^c	2.0 (0.62)	.50	3.05	0.31	-0.01	8.1	1.5	9	31
Saugatucket River RI	SR	14-12-78	41.423	12.3 ^c	3.0 (0.92)	.35	1.40	1.48	-0.40	2.0	1.1	509	16
Wickford RI	WK	15- 3-76	41.566	10.5 ^d	4.7 (1.45)	.35	2.92	0.23	-0.02	4.6	1.4	15 ^j	27
Coonamessett River MA	CR	12- 5-77	41.577	11.0 ^e	4.0 (1.23)	0	1.10	0.59	-0.05	2.7	1.0	101	12
Allen Harbor RI	AH	27- 9-77	41.620	12.4 ^d	4.5 (1.38)	.50	4.20	0.48	-0.03	61.1	1.9	358	28
West Falmouth MA	WF	3- 5-77	41.633	10.5 ^e	5.0 (1.54)	.50	0.46	0.80	0.27	2.1	0.8	190	32
New Bedford MA	NB	18-10-78	41.639	10.5 ^e	4.0 (1.23)	.35	1.39	0.72	0.07	3.0	1.5	567	22
East Greenwich Cove RI	EG	3- 3-76	41.656	11.5 ^d	5.0 (1.54)	.20	2.08	1.08	-0.66	3.6	1.6	24 ^k	19
Bourne MA	BN	22- 5-76	41.682	10.5 ^e	3.8 (1.17)	.50	0.89	0.55	0.01	2.4	0.7	523	30
Watchemoket Cove RI	WC	12- 5-76	41.799	11.1 ^d	5.7 (1.75)	.50	-	-	-	-	-	-	25
Portland ME	PT	21- 7-76	43.636	9.1 ^f	10.4 (3.20)	.50	1.56	1.14	0.11	16.2	2.5	209	27
Deer Isle ME	DI	22- 9-76	44.203	7.4 ^g	11.2 (3.45)	.80	1.90	1.38	0.57	9.8	1.6	24	32
Goose Cove ME	GC	20- 7-76	44.377	7.1 ^h	11.1 (3.42)	.80	-0.51	1.37	0.09	2.8	1.4	254	20
Long Cove, Searsport ME	SP	22- 9-76	44.463	7.1 ^h	11.5 (3.51)	.65	1.52	1.67	0.90	15.9	2.9	135	25
Stockton Harbor ME	SH	13- 9-78	44.464	7.1 ^h	11.5 (3.51)	.65	0.26	2.05	0.15	7.3	1.3	399	25
Perry ME	PY	15- 8-78	44.973	6.7 ^g	21.0 (6.46)	.65	2.22	1.58	-1.38	5.2	2.4	23	30
Robinston ME	RS	15- 8-78	45.106	6.8 ^g	21.0 (6.46)	.65	-0.41	1.53	0.27	9.6	2.2	44	28
Janvrin Lagoon NS	JL	18- 7-78	45.458	9.0 ⁱ	4.0 (1.23)	.65	2.24	0.46	0.06	8.2	1.4	177	29
Potato Island NS	PI	18- 7-78	45.589	9.0 ⁱ	4.0 (1.23)	.65	-0.67	1.58	0.15	10.3	4.6	20	29

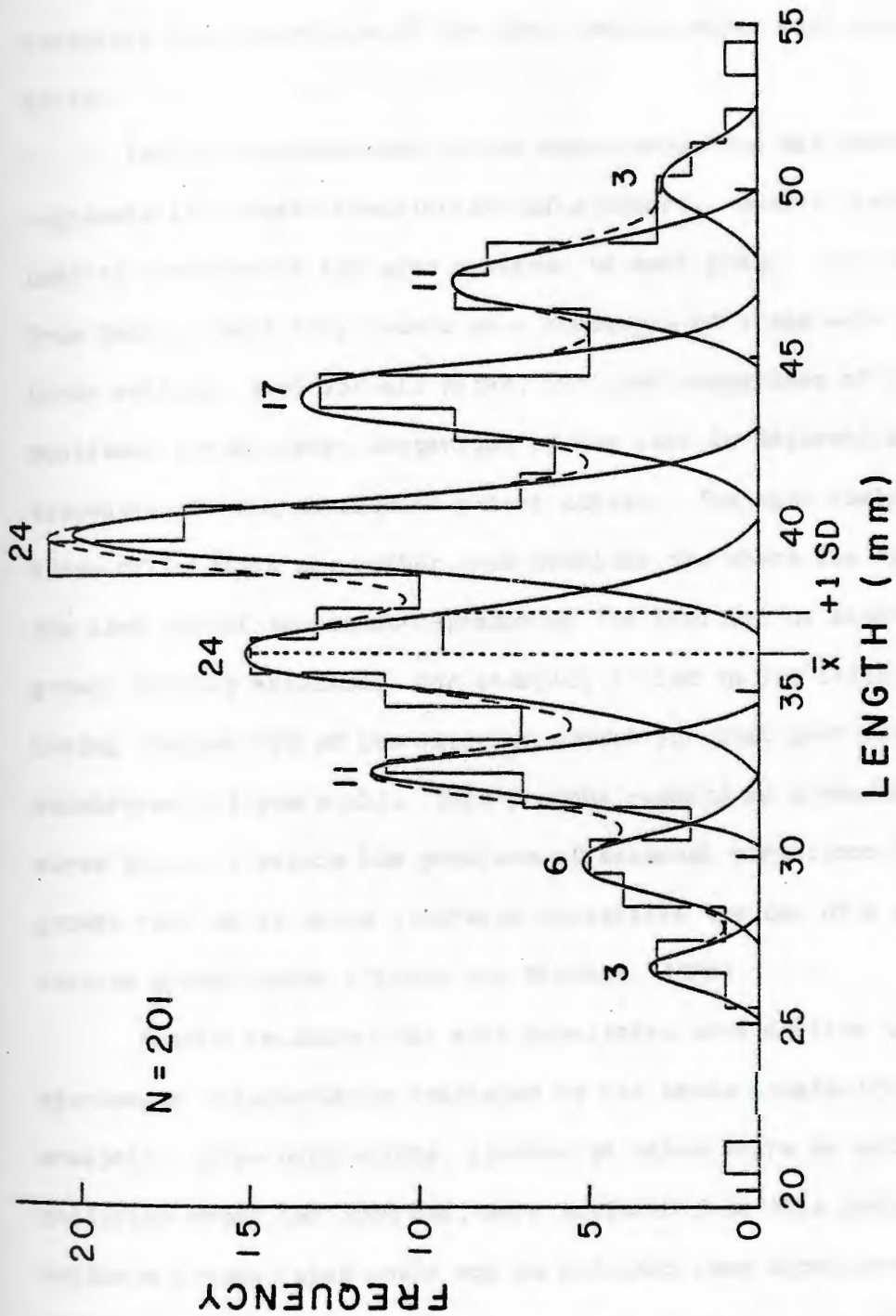
^aBeaven (1960)^bJeffries (1962)^cMarine Research (1975)^dHicks (1963)^eGilbert (1973)^fGilfillan et al. (1976)^gDow (Personal communication)^hShorey (1973)ⁱSamato (1972) and Thomas (1978)^jEstimated from clam tissue concentration^kEstimated from gas chromatography measurement

analysis.

A length-frequency histogram for each population was plotted at 1 mm intervals and the modes on the resulting graph were broken down into a series of normal curves by the Petersen Method (Tesch, 1971; Macdonald and Pitcher, 1979) using a Dupont 310 Curve Resolver. The curve resolver is an analog computer which allows one to break down a complex envelope into its basic components in a graphical fashion. The computer has ten function generator channels each capable of producing a normal curve on a cathode ray tube. The images of these curves can then be projected on to the length-frequency histogram. The histogram can then be broken down left to right in the following manner. The first channel is switched on and the projected curve is positioned such that its location, width, and height correspond to the left edge of the histogram. The remainder of the histogram is then resolved by successively turning on channels and positioning the curves such that the envelope projected (formed by the summation of all the 'on' channels) matches the outline of the histogram. The optical output gives the observer immediate feedback, and repeated trials can be made quickly by varying the size, shape, position, and number of curves until it is felt that a reasonable 'fit' to the data has been obtained. At this point the output of each channel can be turned on and displayed independently, and its projection traced on the histogram. Figure 2 illustrates the results of this process. From the resulting graphs the mean and standard deviation of the normal curve representing each mode of the histogram can be obtained. The mean occurs at the peak and the standard deviation is the half-width at 61% of the height

Figure 2. Mya arenaria. An example of a length-frequency histogram showing the distributions for each age group as determined with the curve resolver. Solid curves = age groups. Dashed curve = total fitted envelope. The mean plus one standard deviation is shown for the fourth curve. Number above represents the percentage of the sample under each curve respectively.





(see curve 4, Figure 2) (Macdonald and Pitcher, 1979). The curve resolver is also equipped with an integrater allowing one to determine the percentage of the whole sample under each component curve.

Each curve generated by the above procedure was assumed to represent the length distribution of a cohort. Several methods were used to corroborate the ages assigned to each group. For samples from Maine, shell ring counts on a subsample of clams were used. Other methods, used for all sites, included comparison of the data to published growth data, comparison of the data to adjacent areas, and inspection of the subsequent growth curves. The ages assigned were those of relative age rather than absolute age where the age beyond the last annual increment represented the fraction of expected yearly growth already obtained. For example, a clam in its fifth year, having reached 50% of its expected growth for that year would be considered 4.5 years old. This process results in a smoother growth curve since it avoids the problems of seasonal variations in the growth rate which would otherwise necessitate the use of a more complex growth model (Cloern and Nichols, 1978).

Growth estimates for each population were derived using the age-length relationships developed by the above length-frequency analysis. Five populations, located at sites where an acute pollution event had occurred, were excluded from this process because reliable growth rates could not be obtained (see Appeldoorn, 1980). Growth was estimated by fitting a von Bertalanffy curve to the data. The growth curve is described by the equation:

$$L = L_{\infty} (1 - e^{-K(t-t_0)})$$

where t = time, L = length at time t , L_{∞} = maximum asymptotic length, K = growth constant, and t_0 = time when $L=0$. According to the methods of Gallucci and Quinn (1979) the model was fitted to the data by nonlinear least-squares regression using the NLIN procedure of SAS79 (Helwig and Council, 1979). The use of such a nonlinear regression procedure is advantageous since not only are estimates of K , L_{∞} and t_0 obtained but estimates of their asymptotic standard errors are also available as well as the correlation coefficient of K and L_{∞} , ($\text{corr}(K, L_{\infty})$). Normal linear curve fitting techniques do not allow for estimates of the variance of the parameters and hence the parameters could not be compared statistically.

After obtaining estimates of the von Bertalanffy parameters the growth function was reparameterized to obtain the single growth parameter ω of Gallucci and Quinn (1979). The parameter is estimated by $\omega = K \cdot L_{\infty}$ and its variance is given as:

$$\text{Var}(\omega) = L_{\infty}^2 \text{Var}(K) + K^2 \text{Var}(L_{\infty}) + 2KL_{\infty} \text{corr}(K, L_{\infty}) \text{Var}(K) \text{Var}(L_{\infty}).$$

Biologically, ω can be interpreted as the instantaneous rate of growth at L_0 . Using a single parameter to represent growth simplifies the testing of growth differences between populations.

Normally when comparing two curves the null hypothesis is H_0 :

$$K_1 = K_2 \text{ and } L_{\infty 1} = L_{\infty 2}.$$

Interpretations become difficult if one equality is rejected and the other is not due to the negative correlation between L_{∞} and K , that is, L_{∞} and K represent some of the

same growth properties. By representing growth with ω one need deal with only one parameter thereby simplifying the comparisons. In addition ω tends to be more robust than either K or L_∞ to variations in the data (Gallucci and Quinn, 1979).

The environmental data listed in Table 1 was subjected to principal components analysis (PCA) in an effort to reduce the observed variables to a more meaningful and manageable number of factors without excessive loss of information. PCA is a statistical technique used to analyze the dependence structure of multivariate data. PCA attempts to locate the hidden factors or components which have generated dependence in the observed variables. In other words, the observed variables are shown to be functions of a smaller number of latent components (Morrison, 1971). These components can then be used to explain variation in the data. The components produced by PCA are (1) independent and (2) ordered such that the first component accounts for most of the observed variation, the second component accounts for most of the remaining variation and so on. The following definitions are used:

Component - a composite variable which is a linear combination of the original variables such that $C_i = b_{i1}X_1 + b_{i2}X_2 + \dots + b_{in}X_n$ where C_i is the i th component, the X 's are the observed variables, and the b 's are the coefficients.

Loading - the degree and direction of the relationship of a variable to its component. They are the coefficients of the component (b_i) and the correlation coefficients (r) between the variables and the component.

Communality - the amount of each variable's variation that is

accounted for by the components.

Percent variance - the amount of variance in the observed variables accounted for by a component.

The analysis was run on the Pearson product-moment correlation matrix of the environmental parameters (to allow for standardization of the units of measurement) using the CORR, FACTOR and SCORE procedures of SAS79 (Helwig and Council, 1979). The factors obtained from PCA were then used to analyze variations in the growth rate ω .

Variations in ω were analyzed using a step-wise functional regression of $\log_{10}(\omega)$ on the components generated by PCA. The analysis was made by calculating the functional regression of $\log_{10}(\omega)$ on Component 1, taking the residuals and regressing them on Component 2, and so on. The geometric mean functional regression was deemed more suitable than the usual predictive regression because of variability in both ω and the components, small sample size, and uncertainties about the distribution of the data (Ricker, 1973). Predictive regression yields a regression coefficient (slope) of b while functional regression yields a regression coefficient of $v = b/r$ where r is the correlation coefficient. The standard error of v (SE_v) is the same as the standard error of b (SE_b). 95% confidence limits on v are approximated by $v \pm 2SE_v$ (Ricker, 1973). The logarithmic transformation of ω was used because the plot of against Component 1 indicated a logarithmic relationship. Estimates of b , r^2 and SE_b were obtained using the GLM procedure of SAS79 (Helwig and Council, 1979). These estimates were used to calculate v and its 95% confidence limits. The significance of the

Regression is tested by seeing if the confidence limits bracket $v=0$. If not, the null hypothesis $H_0: v=0$ is rejected.

RESULTS

For each population the mean length at age as determined through length-frequency analysis is given in Table 2. A von Bertalanffy growth model was then fitted to these data excluding the 5 sites acutely affected by pollution. The model parameters determined by the nonlinear curve fitting process plus the growth parameter ω are presented in Table 3. Using the 95% confidence limits around ω statistically significant growth differences become readily apparent. A regression of ω on latitude (Figure 3) clearly shows a significant latitudinal trend in growth: growth decreases with increasing latitude. Although the regression accounts for most of the observed variation in ω it does not indicate what underlying processes may be responsible for this relationship.

Principal components analysis was used to try and deduce factors which could have contributed to the latitudinal trend and to point out other factors which might be important to growth. These secondary factors could help explain some of the residual variation in growth. The correlation matrix used in the PCA is given in Table 4, and the results of the PCA are shown in Table 5. In order to simplify the table those loadings less than 0.30 have been left out although all variables contribute to all components to some degree. The first five components have been retained and account for 88% of the observed variation. Of these, the first three were examined in

Table 2. *Mya arenaria*. The age (years), length ± 1 standard deviation (mm), and percent of the population for each year class at each site as determined by length-frequency analysis. The sample size for each site is given in parentheses. -: undefined

Age	Length	% of Sample	Age	Length	% of Sample	Age	Length	% of Sample
Quonochontaug Pond-1 (198)			Allen Harbor (144)			Potato Island (201)		
1.33	23.9 ± 2.1	33	1.85	30.0 ± 1.8	11	2.5	25.3 ± 0.7	2
2.33	30.7 ± 2.1	43	2.85	37.7 ± 2.6	24	3.5	30.9 ± 1.3	8
3.33	38.3 ± 1.9	13	3.85	44.5 ± 1.5	15	4.5	34.6 ± 1.6	25
4.33	44.9 ± 1.3	7	4.85	50.4 ± 1.8	18	5.5	39.2 ± 1.5	41
5.33	49.6 ± 1.2	2	5.85	55.2 ± 1.3	14	6.5	43.7 ± 1.0	13
6.33	54.2 ± 1.4	3	6.85	59.7 ± 1.4	8	7.5	47.1 ± 0.8	6
7.33	58.6 ± 1.4	1	7.85	65.8 ± 1.4	9	8.5	49.4 ± 0.9	3
Watchemoket Cove (90)			East Greenwich Cove (192)			Robinston (190)		
1.15	27.6 ± 2.9	24	1.0	20.8 ± 3.5	30	3.67	37.9 ± 1.6	8
2.15	34.8 ± 2.0	31	2.0	30.8 ± 1.0	9	4.67	42.5 ± 1.6	16
3.15	42.4 ± 1.7	19	3.0	38.4 ± 2.8	49	5.67	47.2 ± 1.6	41
4.15	48.2 ± 2.5	11	4.0	45.0 ± 1.5	11	6.67	51.7 ± 1.0	20
6.15	57.1 ± 1.4	8	5.0	50.9 ± 1.1	3	7.67	54.6 ± 0.9	7
7.15	62.5 ± 1.0	6				8.67	57.0 ± 1.2	4

Table 2. Continued.

Age	Length	% of Sample	Age	Length	% of Sample	Age	Length	% of Sample
Quonochontaug Pond-2 (146)			Bourne (187)			Goose Cove (101) ^a		
2.15	33.7 \pm 2.7	41	1.15	22.7 \pm 2.2	8	3.0	24.1 \pm 1.9	7
3.15	41.6 \pm 2.0	28	2.15	30.6 \pm 2.4	5	4.0	34.3 \pm 3.8	12
4.15	49.0 \pm 1.3	6	3.15	40.8 \pm 2.4	14	5.0	36.4 \pm 4.1	25
5.15	55.1 \pm 1.8	6	4.15	48.2 \pm 2.3	27	6.0	39.6 \pm 3.2	23
6.15	60.2 \pm 1.0	4	5.15	54.4 \pm 1.3	10	7.0	46.6 \pm 9.8	5
7.15	65.8 \pm 1.3	6	6.15	58.9 \pm 1.5	9	8.0	47.7 \pm 17.2	17
8.15	70.5 \pm 0.8	4	7.15	64.3 \pm 2.1	12	9.0	55.2 \pm 6.9	6
9.15	73.5 \pm 0.8	3	8.15	70.5 \pm 1.3	8	10.0	61.5 \pm 2.1	2
10.15	79.0 \pm 1.1	4	9.15	75.7 \pm 2.0	3	11.0	59.5 \pm 5.8	4
Saugatucket River (140)			West Falmouth (183)			Long Cove, Searsport (152)		
2.0	29.0 \pm 1.3	2	1.15	28.6 \pm 2.6	9	6.2	38.0 \pm 0.6	2
2.6	33.8 \pm 0.9	5	2.15	38.8 \pm 2.6	3	7.2	41.5 \pm 1.4	3
3.0	37.6 \pm 1.6	9	3.15	45.2 \pm 1.5	2	8.2	44.9 \pm 1.0	6
3.8	43.3 \pm 2.2	42	4.15	53.3 \pm 2.9	27	9.2	47.2 \pm 0.6	5
4.8	48.9 \pm 1.5	7	5.15	61.6 \pm 1.5	8	10.2	49.9 \pm 1.0	14
5.8	52.8 \pm 1.1	12	6.15	68.2 \pm 1.9	20	11.2	53.0 \pm 1.2	15
7.0	56.1 \pm 0.7	6	7.15	73.4 \pm 1.7	7	12.2	55.3 \pm 0.7	11
8.0	60.0 \pm 1.2	6	8.15	78.8 \pm 1.4	5	13.2	57.0 \pm 0.8	10
9.0	64.5 \pm 1.2	3	9.15	84.5 \pm 2.6	1	14.2	59.0 \pm 0.9	18

^a Ages determined by counting shell rings

Table 2. Continued.

Age	Length	% of Sample	Age	Length	% of Sample	Age	Length	% of Sample
New Bedford (180)			Stockton Harbor (164)			Winnapaug Pond (229)		
1.85	32.0 \pm 1.0	0.5	3.0	31.0 \pm 1.8	2	0.9	24.2 \pm 1.6	3
2.85	43.7 \pm 1.2	3	4.0	38.2 \pm 1.8	2	1.5	31.5 \pm 1.0	2
3.56	48.3 \pm 1.6	8	5.0	44.8 \pm 1.4	11	1.9	37.4 \pm 1.2	5
3.85	51.2 \pm 0.8	15	6.0	49.2 \pm 1.1	13	2.5	41.4 \pm 1.2	7
4.56	53.9 \pm 0.9	16	7.0	54.1 \pm 1.5	17	2.9	46.2 \pm 1.3	14
4.85	56.2 \pm 0.9	21	8.0	58.2 \pm 1.2	21	3.5	50.6 \pm 1.8	24
5.56	58.9 \pm 1.2	16	9.0	62.8 \pm 1.3	13	4.5	56.0 \pm 1.6	29
5.85	61.2 \pm 0.8	11	10.0	66.5 \pm 1.4	11	5.5	60.5 \pm 1.2	8
6.85	64.4 \pm 0.9	6	11.0	70.3 \pm 1.2	3	6.5	64.1 \pm 1.4	4
7.85	69.0 \pm 0.6	3	12.0	75.0 \pm 1.3	5	7.5	67.2 \pm 0.7	4
Raritan Bay (200)			Tangier Sound (166)			Big Annemessex River (177)		
1.33	30.4 \pm 0.8	3	1.33	54.6 \pm 2.3	36	1.33	57.0 \pm 1.3	14
1.67	36.4 \pm 1.8	23	2.33	67.9 \pm 1.2	13	2.33	68.8 \pm 2.0	33
2.33	40.2 \pm 1.7	39	3.33	78.2 \pm 0.9	3	3.33	77.2 \pm 1.3	7
2.67	43.8 \pm 1.6	25	4.33	86.2 \pm 0.7	2	4.33	86.8 \pm 1.5	2
3.33	47.4 \pm 0.8	10						

Table 2. Continued.

Age	Length	% of Sample	Age	Length	% of Sample	Age	Length	% of Sample
Navesink River (103)			Coonamessett River (124)			Portland (367)		
0.67	26.0 ± 2.3	3	1.15	34.0 -	0.5	1.5	19.0 ± 0.8	1
1.33	35.2 ± 2.5	14	2.15	42.8 ± 2.0	4	2.5	26.7 ± 1.3	4
1.67	42.5 ± 2.0	23	2.85	52.0 ± 1.0	7	3.5	31.5 ± 1.6	17
2.33	47.3 ± 1.8	18	3.15	56.1 ± 2.0	7	4.5	37.1 ± 1.6	21
2.67	51.8 ± 1.4	10	4.15	64.0 ± 1.4	18	5.5	41.3 ± 1.6	29
3.33	55.3 ± 1.4	11	5.15	69.4 ± 1.2	9	6.5	44.5 ± 1.2	10
3.67	59.6 ± 1.6	2	6.00	72.8 ± 1.2	16	7.5	48.1 ± 1.2	15
4.50	62.1 ± 1.4	2	7.15	77.4 ± 1.2	18	9.5	52.7 ± 0.7	3
5.50	65.4 ± 1.2	2	8.15	82.3 ± 1.4	17	10.5	55.0 ± 0.5	1
6.50	69.7 ± 1.5	4	10.15	88.2 ± 1.1	5	11.5	56.7 ± 0.4	1
8.50	74.7 ± 1.2	4	11.15	94.0 -	0.5	13.5	60.2 ± 0.5	1
9.50	78.0 ± 1.2	6						

Table 2. Continued.

Age	Length	% of Sample	Age	Length	% of Sample	Age	Length	% of Sample
Perry (180)						Janvrin Lagoon (201)		
3.67	36.4 \pm 1.5	3	4.80	68.1 \pm 2.5	36	3.5	21.0 -	0.5
4.67	41.1 \pm 1.5	11	5.80	75.1 \pm 1.8	13	4.5	26.7 \pm 0.7	3
5.67	47.1 \pm 1.8	29	6.00	80.2 \pm 1.1	7	5.5	29.9 \pm 0.9	6
6.67	55.2 \pm 2.3	46	7.00	84.7 \pm 0.9	2	6.5	32.6 \pm 0.8	11
7.67	62.3 \pm 0.8	5	8.00	88.5 \pm 0.6	2	7.5	36.2 \pm 1.3	24
8.67	66.9 \pm 0.8	3	Deer Isle (318)			8.5	39.7 \pm 1.0	24
9.67	70.9 \pm 1.9	3	3.0	25.7 \pm 1.9	4	9.5	43.8 \pm 1.0	17
Wickford (203)			4.0	31.2 \pm 1.1	7	10.5	47.4 \pm 1.0	11
0.20	7.0 -	0.5	5.0	35.2 \pm 1.3	21	11.5	50.3 \pm 1.0	3
2.00	37.3 \pm 1.1	2	6.0	39.2 \pm 1.3	18	12.5	54.0 -	0.5
2.67	48.7 \pm 1.4	4	7.0	42.1 \pm 1.1	9			
3.00	53.9 \pm 1.4	10	8.0	44.6 \pm 1.0	10			
3.80	60.4 \pm 1.8	18	9.0	47.8 \pm 1.0	12			
			10.0	51.5 \pm 1.0	9			

Table 3. *Mya arenaria*. Estimates and standard errors for the von Bertalanffy constants.

Site Num- Code ber	k	L_{∞}	t_0	Corr($k \cdot L_{\infty}$)	ω	95% Confidence Interval on ω
TS 90	.2530 (.0597)	111.05 (11.18)	-1.188 (.263)	-.9927	29.108	25.218 - 32.997
AR 99	.2740 (.0520)	107.13 (7.22)	-1.440 (.268)	-.9897	29.354	26.096 - 32.612
NR 101	.3016 (.0162)	79.69 (1.10)	-0.718 (.095)	-.8764	24.034	22.250 - 25.819
RB 200	.1829 (.0986)	81.50 (22.08)	-1.450 (.558)	-.9983	14.906	13.190 - 16.623
WP 228	.2992 (.0114)	73.27 (0.89)	-0.400 (.058)	-.9575	21.966	21.150 - 22.782
Q1 202	.1175 (.0194)	93.23 (9.20)	-1.104 (.148)	-.9936	10.954	9.656 - 12.253
Q2 150	.1069 (.0134)	111.00 (6.96)	-1.205 (.191)	-.9920	11.866	10.104 - 13.628
SR 129	.2119 (.0229)	72.34 (2.48)	-0.445 (.225)	-.9737	15.329	13.859 - 16.799
WK 191	.1811 (.0155)	111.80 (4.21)	-0.436 (.127)	-.9833	20.258	18.723 - 21.793
CR 127	.1997 (.0114)	97.75 (1.60)	-0.990 (.143)	-.9728	19.521	17.832 - 21.209
AH 144	.0903 (.0184)	113.20 (13.11)	-1.668 (.288)	-.9967	10.222	8.217 - 12.227
WF 139	.0917 (.0162)	136.73 (14.88)	-1.357 (.184)	-.9964	12.538	10.129 - 14.948
NB 179	.1532 (.0198)	89.28 (4.30)	-1.571 (.304)	-.9922	13.678	12.309 - 15.046
EG 196	.1377 (.0425)	91.95 (18.20)	-0.914 (.186)	-.9974	12.662	11.064 - 11.259
WC 89	.1411 (.0246)	87.18 (7.37)	-1.549 (.236)	-.9894	12.301	9.919 - 14.683
PT 379	.1468 (.0077)	67.91 (1.39)	-0.836 (.122)	-.9734	9.967	9.501 - 10.438
DI 287	.1255 (.0114)	67.96 (2.46)	-0.781 (.218)	-.9911	8.533	7.896 - 9.170
SH 159	.0565 (.0083)	135.71 (12.34)	-0.980 (.336)	-.9973	7.668	5.838 - 9.497
RS 182	.1623 (.0287)	73.13 (4.52)	-0.745 (.434)	-.9910	11.896	10.654 - 13.084
PI 196	.0986 (.0248)	81.55 (10.78)	-0.171 (.432)	-.9958	8.041	6.806 - 9.276

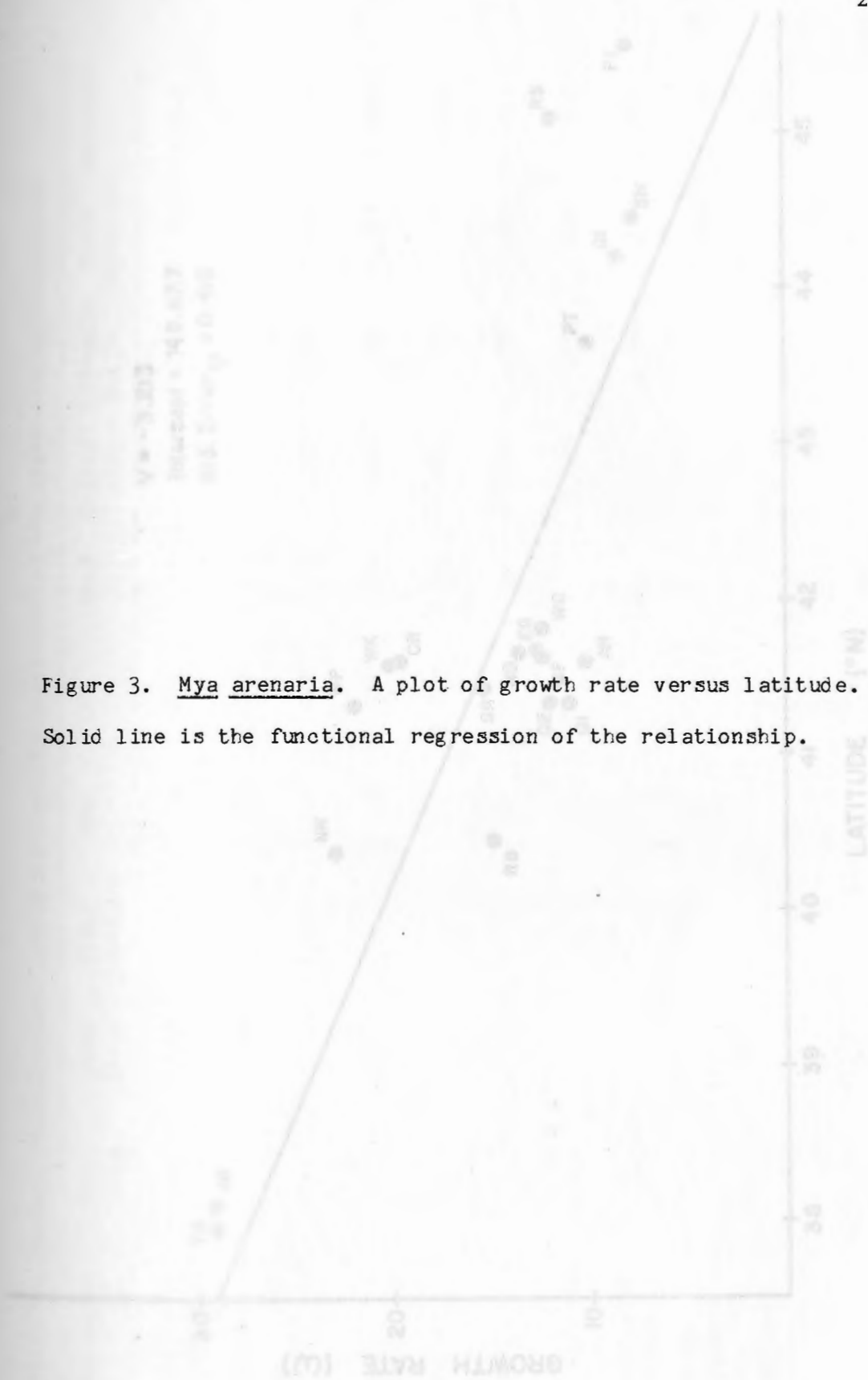


Figure 3. Mya arenaria. A plot of growth rate versus latitude. Solid line is the functional regression of the relationship.

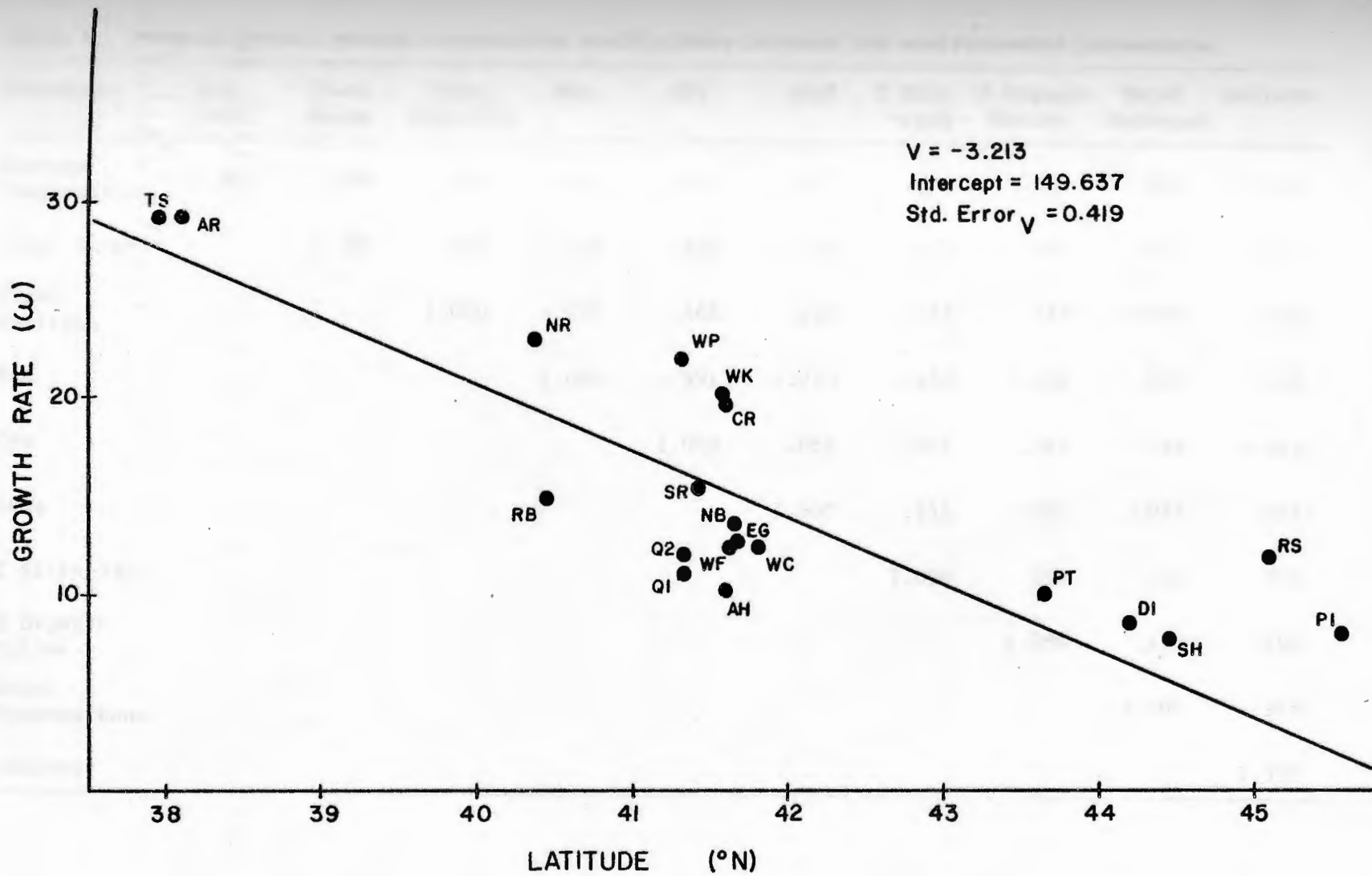


Table 4. Pearson product-moment correlation coefficients between the environmental parameters.

Parameter	Ave. Temp.	Tidal Range	Tidal Position	Md ϕ	QD ϕ	Skq ϕ	% Silt-clay	% Organic Matter	Total Hydrocar.	Salinity
Average Temperature	1.000	-.789	-.763	.438	-.743	-.187	-.090	-.314	-.014	-.343
Tidal Range		1.000	.539	-.278	.656	-.110	.059	.301	-.091	.232
Tidal Position			1.000	-.239	.468	.292	.149	.327	-.050	.553
Md ϕ				1.000	-.591	-.250	.458	-.164	-.040	.259
QD ϕ					1.000	.051	-.041	.365	-.189	-.003
Skq ϕ						1.000	.141	.082	-.053	.011
% Silt-clay							1.000	.258	.226	.215
% Organic Matter								1.000	-.184	.298
Total Hydrocarbons									1.000	-.365
Salinity										1.000

Table 5. Results of the principal components analysis on environmental data. Loadings less than 0.30 have been omitted for clarity.

Environmental Parameter	Principal Components					Communality
	1	2	3	4	5	
Average temperature	-.938					.925
Tidal range	.806			.383		.819
Tidal position	.817					.855
Md ϕ	-.503	.725				.891
QD ϕ	.808	-.382				.872
Skq ϕ			.386	-.858		.933
% silt-clay		.609	.675			.880
% organic matter	.521				.765	.942
Total hydrocarbons			.802			.855
Salinity	.396	.750				.840
Eigenvalues	3.588	1.875	1.363	1.134	0.851	
% variance	35.9	18.7	13.6	11.3	8.5	
% cumulative variance	35.9	54.6	68.3	79.6	88.5	

greater detail for purposes of reification and further analysis.

The first component is interpreted as representing latitude since the major contributing variables vary with latitude. Average annual temperature, as might be expected, shows the highest correlation to this component. It decreases with latitude. Tidal range, tidal position, sediment grain size, variability, and organic matter are all positively associated with latitude. To avoid confusion this component will be referred to as 'northness'. The second component is interpreted as siltiness of the sediment. Grain size (negatively correlated) and percent silt-clay (positively correlated) are the main contributing variables. The high correlation of salinity may reflect the role of flocculation and estuarine circulation in the distribution of silts and clays in estuarine sediments (Krumbein and Sloss, 1963; Knaus, 1978). The third component, positively correlated with hydrocarbons and percent silt-clay, is interpreted as representing sedimentary hydrocarbons. The small grain size indicated by the percent silt-clay, and to some degree by positive skewness, can allow for a greater sedimentary surface area for the retention of hydrocarbons (Lytle and Lytle, 1977).

These three components (northness, siltiness, sedimentary hydrocarbons) were then used for the further analysis of growth through step-wise regression. Several sites were omitted from this analysis because missing values precluded the calculation of the component scores. For this analysis the $\log_{10}(\omega)$ was regressed against northness, the residuals from this regression were regressed against siltiness, and residuals from this second regression were

regressed against sedimentary hydrocarbons. The component scores and residuals are given in Table 6. The results of the analysis are given in Table 7 and Figures 4, 5 and 6. As expected, growth was found to be negatively correlated with northness. The second regression showed a negative relationship between siltiness and growth. The last regression indicated that growth was negatively correlated with sedimentary hydrocarbons. Much of the deviation about this regression is due to the abnormally high values for Allen Harbor.

DISCUSSION

The use of many length-frequency analysis techniques for the determination of age structure and growth is not straightforward. Macdonald and Pitcher (1979) consider the lack of reproducibility as its major drawback. This results from the difficulty in properly distinguishing all the modes in a distribution, especially when multiple spawnings occur or sample size is low. As such, the results of analysis can depend, in large part, upon the experience of the observer. This is not only evident in the resolution of the distribution mixtures but also in the assignment of ages to the various modes. In this respect, however, even the more sophisticated curve resolving techniques are limited since independent estimates of the number of modes present and length at age are usually required. However, length-frequency analysis has proven itself to be a useful and informative technique and the results obtained here are generally reliable.

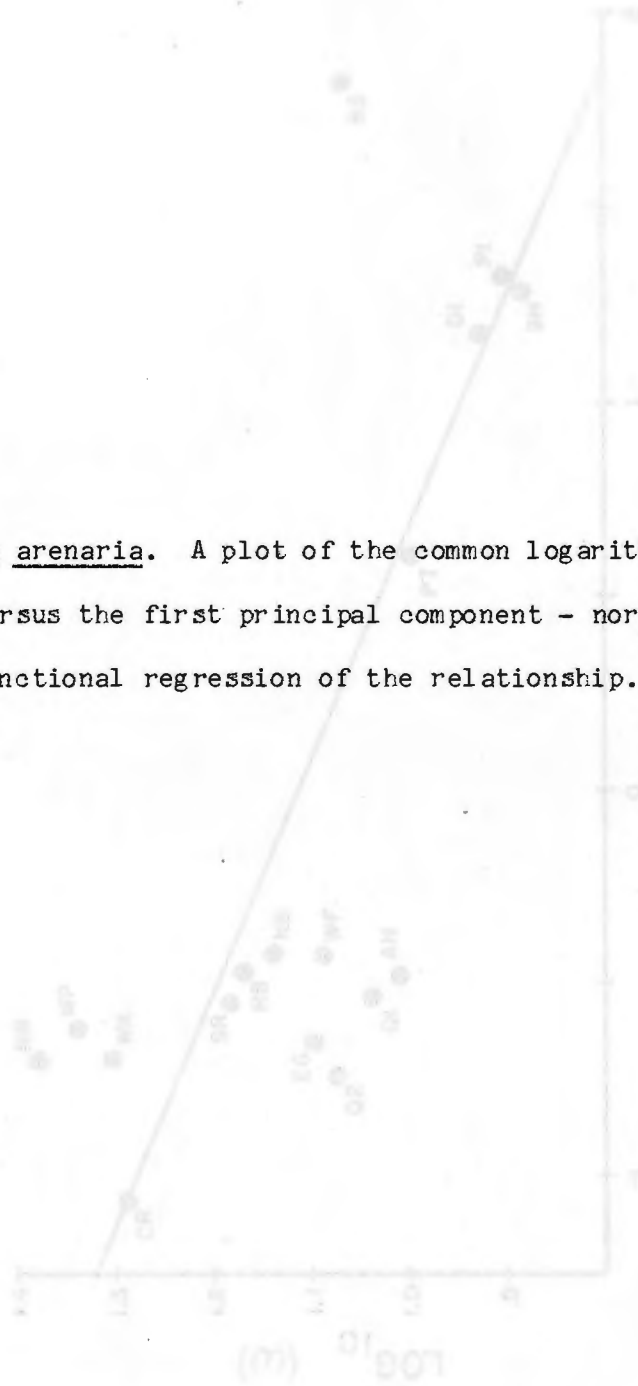
Table 6. *Mya arenaria*. Component scores for the first three principal components plus the logarithm and residuals of ω . -: missing value

Site Code	Northness	Siltiness	Sedimentary Hydrocarbons	Log ω	1st Residual of ω	2nd Residual of ω
NR	-0.701	0.187	-0.525	1.138	.151	.183
RB	-0.471	0.691	-0.380	1.173	-.018	.070
WP	-0.619	0.508	-0.846	1.342	.126	.194
Q1	-0.536	0.257	-1.080	1.040	-.163	-.123
Q2	-0.736	1.305	-0.598	1.074	-.161	-.004
SR	-0.558	-1.352	1.023	1.186	-.020	-.160
WK	-0.065	0.850	-0.689	1.307	.079	.185
CR	-1.065	-1.111	-0.259	1.290	.001	-.112
AH	-0.483	2.473	2.864	1.010	-.184	.103
WF	-0.431	-1.746	0.518	1.095	-.087	-.272
NB	-0.428	-0.742	1.316	1.136	-.048	-.120
EG	-0.651	-0.239	-0.910	1.102	-.119	-.134
BN	-0.146	-0.008	-0.739	-	-	-
PT	0.602	0.402	0.427	0.997	-.016	.040
DI	1.175	0.721	-0.094	0.931	.012	.103
GC	1.165	-1.152	0.220	-	-	-
SP	1.391	0.257	0.900	-	-	-
SH	1.291	-1.047	0.953	0.885	-.016	-.121
PY	1.380	0.643	-1.636	-	-	-
RS	1.824	-0.309	-0.485	1.074	.262	.239
JL	-0.042	0.729	0.082	-	-	-
PI	1.328	0.145	-0.452	0.905	.011	.038

Table 7. Mya arenaria. Results of the stepwise regression of growth (ω) on the first three principal components. The slope of the predictive regression (b) can be found by $b=v \cdot r$

Regression	r	Intercept	v=slope	Approximate 95% Confidence Limits
$\text{Log}_{10}(\omega)$ vs Northness	.693	1.1137	-.1653	-.2269 < v < -.1037
1st residual vs Siltiness	.184	-0.0112	-.1116	-.1682 < v < -.0549
2nd residual vs Sedimentary Hydrocarbons	.217	0.0065	-.1472	-.2214 < v < -.0730

Figure 4. Mya arenaria. A plot of the common logarithm of the growth rate versus the first principal component - northness. Solid line is the functional regression of the relationship.



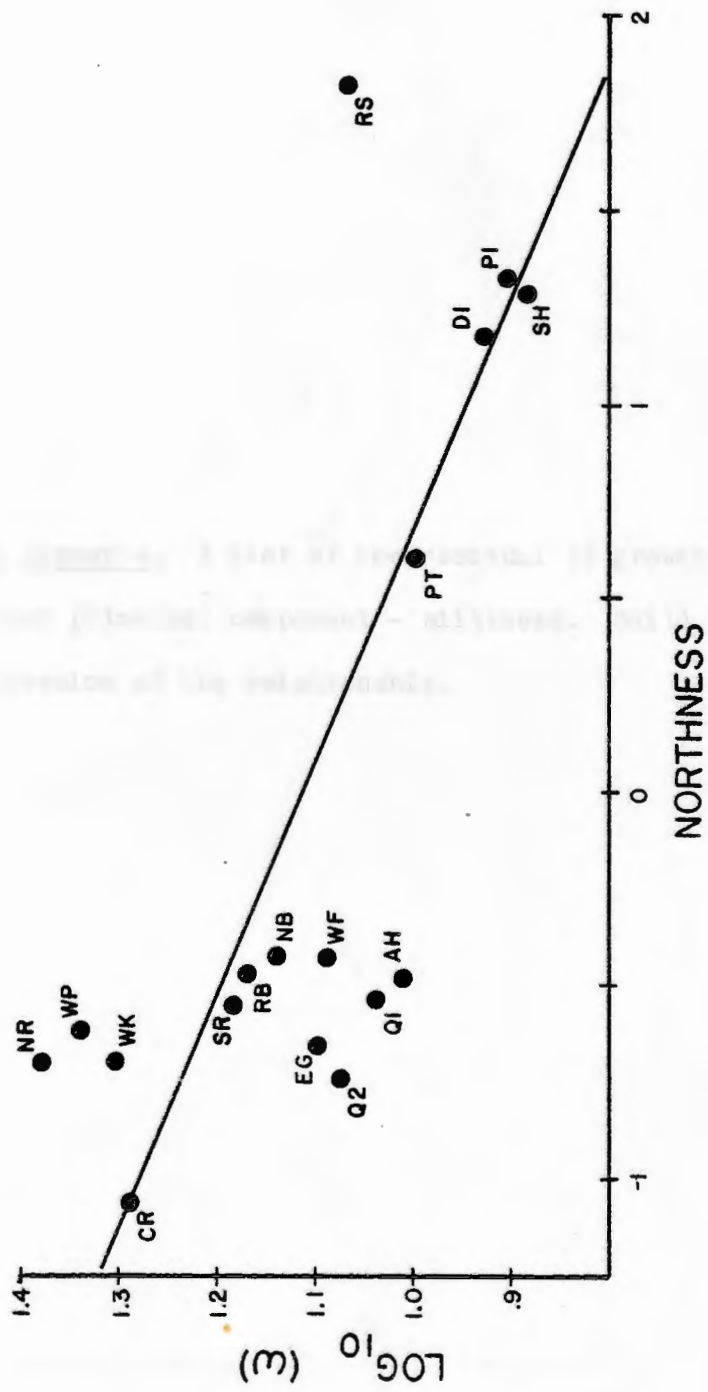
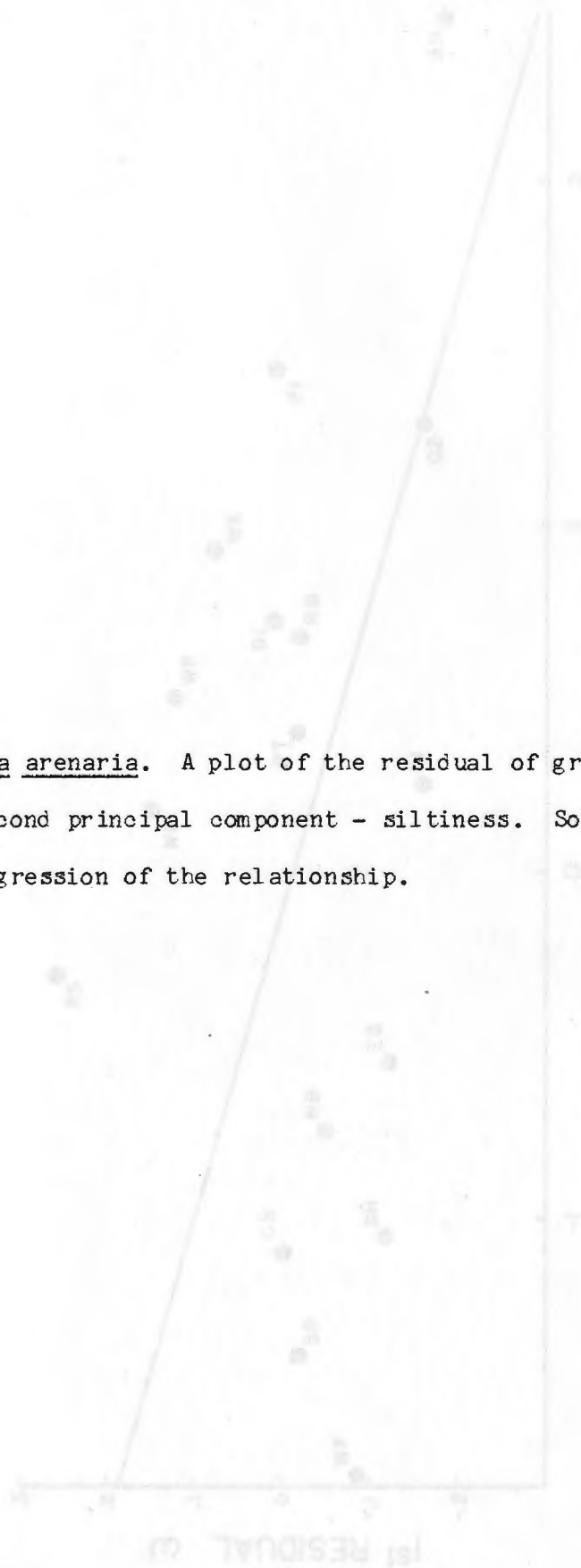


Figure 5. Mya arenaria. A plot of the residual of growth rate versus the second principal component - siltiness. Solid line is the functional regression of the relationship.



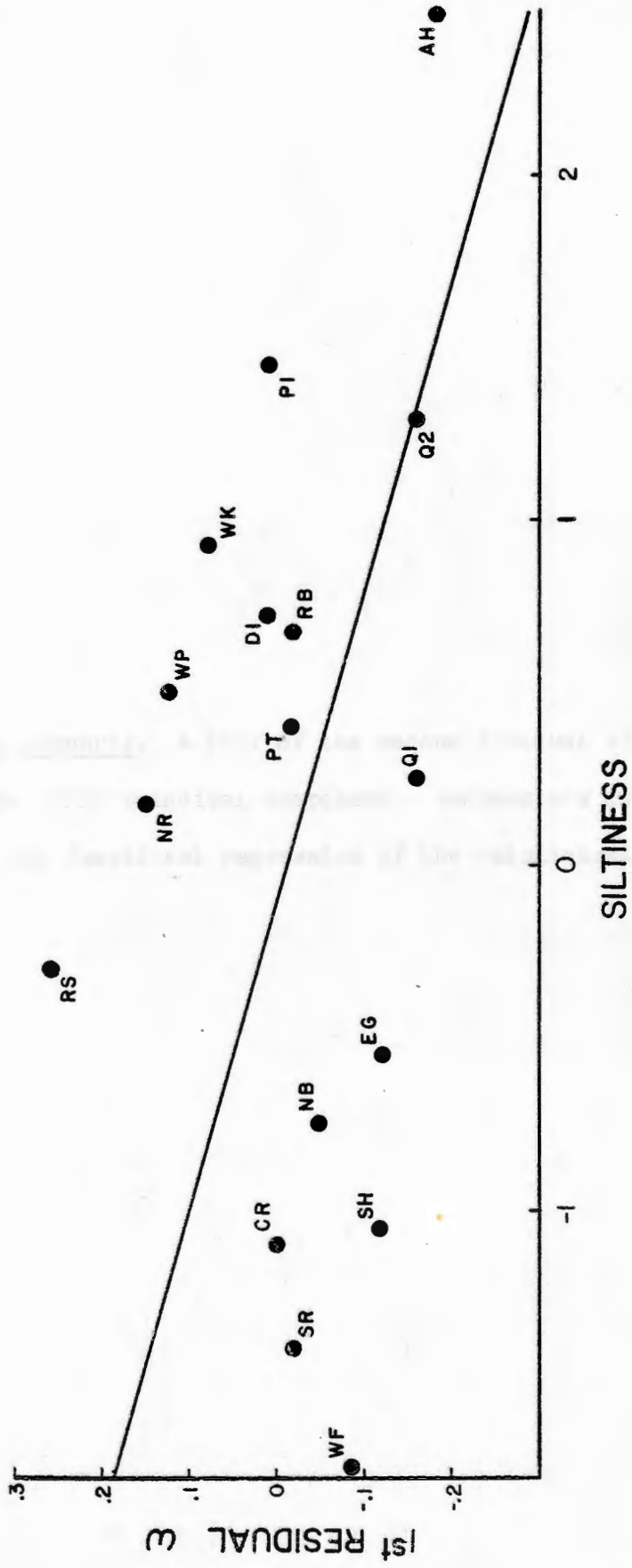
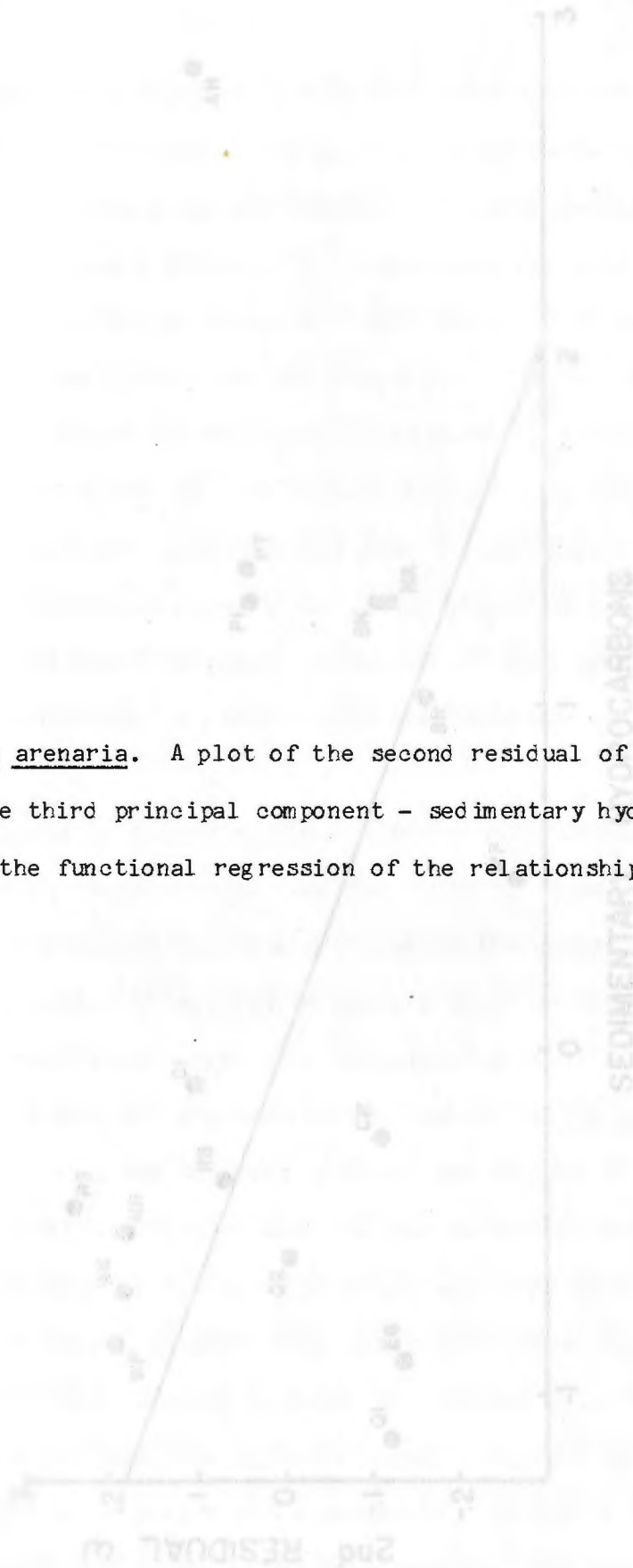
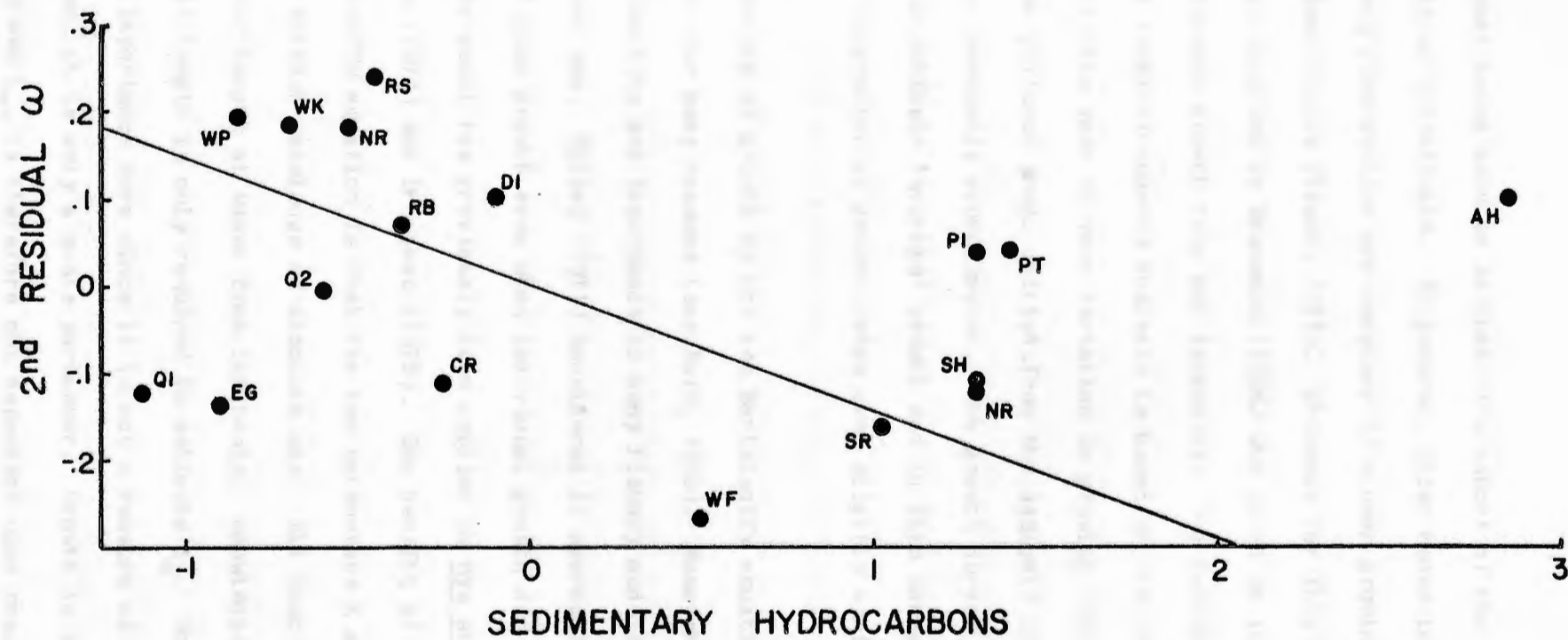


Figure 6. Mya arenaria. A plot of the second residual of growth rate versus the third principal component - sedimentary hydrocarbons. Solid line is the functional regression of the relationship.





The growth being modeled is that of a cohort of the population, not of individuals. In general, older modes in a length-frequency distribution are composed of slower growing but longer lived individuals (Tesch, 1971). Evidence for this trend in Mya arenaria is supplied by Newcombe (1936) who found an inverse relationship between growth rate and longevity. The determination of growth through length-frequency analysis is based on the assumption that there is little year to year variation in growing conditions. Except in those polluted areas omitted from the analysis this assumption was reasonably approximated. The growth curves obtained are designed to estimate 'average' growth and in this sense they represent an integration of growth rates over slightly varying conditions.

The modeling of growth by the von Bertalanffy equation has been criticized for many reasons (see Roff, 1980). However, its general applicability and importance to many fishery models have led to its continued use. Dickey (1971) considered it appropriate for modeling population growth even when individual growth did not fit the model. The model has previously been applied to Mya arenaria by Munch-Petersen (1973) and Brouseau (1978). One benefit of applying the von Bertalanffy equation is that the two parameters K and L can be determined without knowledge of absolute age. All that is needed are estimates of length at known time intervals. Knowledge of absolute age at length is only required to estimate t_0 . However, t_0 is of less importance here since it is not a measure of growth. Indeed, it is only a scale parameter. Growth in this study, as measured by $\omega = K \cdot L_{\infty}$, is therefore not dependent upon possible

inaccuracies in the assignment of ages to modes of the length-frequency distribution.

The parameter ω proved to be a suitable measure of growth in this study. By reducing the description of growth to a single parameter the discrimination and interpretation of growth rate differences was simplified. In addition, ω easily lent itself to further analysis, using more sophisticated techniques, since its simplicity made it more tractable to manipulation and interpretation. As with any parameter, the limits of ω are dependent upon the quality of the original data. In the present study it was impossible to determine how much of the variation in ω was due to inaccuracies in the data. However, after three regressions the variation in ω due to errors of measurement was approaching a 'significant' proportion of the remaining total variation and further regressions would have been suspect.

The observed relationship between latitude and growth is not surprising, especially considering the range of temperatures reflected in the data. Increasing growth would be expected at higher temperatures due to temperature's direct effect on metabolism and length of the growing season (Brouseau, 1979). In addition, with increasing temperature Mya is found lower intertidally or even subtidally, thereby increasing its daily feeding period. However, Belding (1930), Dow and Wallace (1961), Newcombe and Kessler (1936), and Swan (1952) have stated that local hydrologic and edaphic conditions are more important than temperature in affecting growth; and previous studies have failed to firmly establish such a latitudinal relationship. Newcombe (1936) noticed growth differences

between three widely separated sites which he attributed to temperature differences. Turner (1948) made a similar observation also based on three areas. Brouseau (1978) showed a tendency for populations in Massachusetts to grow faster than more northerly populations but the relationship was not definite. Each of these studies suffered from two deficiencies: (1) small sample size and (2) limited geographical range. Under these conditions variations in growth due to local conditions can mask any latitudinal trends. The wide variation of points around the regression line in Figure 3 gives evidence for this.

Principal components analysis proved to be useful in the further detailed analysis of growth. PCA produced a smaller number of meaningful variables, which were easily interpretable, and when used for further analysis produced lucid and rational results.

The first component, northness, correlated well with growth. Again this is not surprising. Temperature had the highest loading for this component and its influence on growth has already been discussed. Tidal position, as mentioned, is a secondary result of temperature variations. As with many factors, the components produced by PCA represent an integration of effects and the correlation between growth and northness may also be dependent upon factors other than temperature. The increase in tidal range with northness, due to the large tides of the Gulf of Maine and the Bay of Fundy represents to some degree an increase in tidal current. Belding (1930) considered current the most important factor pertaining to growth. Current, in turn, can also influence edaphic conditions. Hence a coarse but variable grain size distribution is

associated with northness. The coarser sediments found toward the north are also a reflection of their glacial origins; and they are beneficial in their own right since they allow for ample water percolation, drainage and exchange (Dow and Wallace, 1961; Swan, 1952). Within northness, then, there are two sets of opposing conditions which influence growth. Temperature is positively associated with growth while current and sediment characteristics are negatively associated with growth. Since northness is itself negatively correlated with growth it must be concluded that the effects of temperature are overriding and dominant.

The relationship between northness and w was logarithmic in nature. Since temperature dominates the relationship this result is reasonable. The effect of temperature on metabolic systems is known to be exponential in nature (Gunter, 1957). What requires explanation is the linear relationship between growth and latitude. It is felt that the addition of the two Maryland sites in the growth-latitude graph unjustly extends the relationship since the large change in latitude may not be accompanied by equally large changes in ecological conditions. In this case northness should be a more proper representation of the geographical variation in conditions than is latitude.

The effect of the second component, siltiness, on growth also represents an integration of processes. In small quantities silt and clay help to stabilize surface sediments (Kellogg, 1905) but in large quantities they become detrimental. Sanders (1958) found that the distribution of filter feeders, in general, was limited by the silt-clay content of the sediment. Studies with Mya have shown that

excessive siltation can reduce feeding, through clogging of the gills (Belding, 1930), or lead to complete smothering and death (Wilton and Wilton, 1929; Dow and Wallace, 1961). Silty sediments also tend to be fairly consolidated and reduced growth has been observed in such sediments (Swan, 1952; Dow and Wallace, 1961). Silt can easily become trapped between the shell and mantle, with a consequent interruption of growth (Shuster, 1951). Small grain size is also an indication of a poor current regime, itself a contributing factor to reduced growth. The negative correlation found between siltiness and growth is, therefore, logical and consistent with previous reports.

Sedimentary hydrocarbons, the third component derived from the PCA, was also negatively associated with growth. Many studies have shown that the growth of Mya is adversely affected by the presence of petroleum hydrocarbons (Dow, 1975; Dow and Hurst, 1975; Gilfillan and Vandermeulen, 1978; Gilfillan et al., 1976; Appeldoorn, 1980). Hydrocarbon pollution can adversely affect growth through direct toxicity, smothering, and sediment compaction.

The components identified through PCA have been shown to influence growth. However, these should not be considered the only factors. PCA is limited by the input data and can only reflect the factors represented by that data. In the present study no direct measurements were made on current flow, food supply, and a number of other important factors. Estimates of tidal range, sediment size, etc. can account for only some of these factors. In general the study supported the use of PCA for the analysis of ecological systems. The three components identified accounted for much of the growth differences between the sites and the component loadings revealed the

integration of processes within each component.

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THE EFFECTS OF POPULATION GROWTH RATE IN THE
FISH, *SCOPelogadus*, TO THE GROWTH AND
MORTALITY OF POLLUTION

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ABSTRACT

length-frequency analysis was used to generate age-length curves for six populations of the soft-shell clam, Mya arenaria, exposed to a range of pollution levels. Five of the populations were each subjected to a single oil spill. The sixth population was subjected to the onset of pollution. This was accompanied by a noticeable break in the age-length curve representing a decrease in the population growth rate following the onset of pollution. At the site where the onset occurred the age-length curve showed a similar break indicating the resumption of near normal growth. An attempt is made to relate the severity and persistence of the pollution effect on growth to the degree of pollution in the age-length curve. A method whereby pre-pollution growth can be estimated is presented and applied to two populations.

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ABSTRACT

Length-frequency analysis was used to generate age-length curves for six populations of the soft-shell clam, Mya arenaria, exposed to a sudden pollution event. Five of the populations were each subjected to a single oil spill. The sixth population was subjected to the onset and subsequent abatement of the effluent from a heavy metals mine. With one exception, where no effect was noticed, the onset of pollution was accompanied by a noticeable break in the age-length curve representing a decrease in the population growth rate following the event. At the site where abatement occurred the age-length curve showed a second break indicating the resumption of near normal growth. An attempt is made to relate the severity and persistence of the pollution effect on growth to the degree of deflection in the age-length curve. A method whereby pre-pollution growth can be estimated is presented and applied to two populations.

INTRODUCTION

The need for more information on the effects of discharging pollutants into marine ecosystems has long been recognized. However, only recently has significant progress been made toward this end. Early investigators studied only acute lethal effects, and the variability in the number and reliability of the methods involved led to much confusion (Hyland and Schneider, 1976). With improving methodology there has been an increase in the interest of investigating chronic and sublethal effects (Anderson, 1977). This has been coupled with the recognition that research should be concerned with effects on population processes rather than on individuals (Vanderhorst et al., 1978). Notable studies involving the long term monitoring of populations following a pollution event are those of the West Falmouth oil spill, the Chedabucto Bay oil spill, and studies of pulp mill effects in Sweeden (Rosenberg, 1976). One major problem in studying the effects of sudden environmental changes is the availability of reliable control data from either measurements made prior to the change or from a suitable control area.

Recently an investigation into the status of soft-shell clam (Mya arenaria) populations and their relationship to various forms of pollution has taken place (Brown et al., 1979). Within the context of this investigation samples were collected from several sites characterized by a sudden change in environmental quality due to the onset or abatement of pollution. Population growth has been one of the parameters studied for each site. The effect of each pollution event on growth was obviously of particular interest.

The purpose of this paper is primarily to present age-length curves of soft clam populations from the sample sites where a pollution event occurred. Based on a few assumptions these curves can be used to represent growth. It will be shown that a sudden change in the environmental quality resulting from the onset or abatement of pollution is reflected by a shift in the age-length curve. In addition, a method will be presented whereby growth prior to a pollution event may be estimated.

METHODS

The growth of clams was studied at six sites where a discrete pollution incident (either onset or abatement) occurred. Five of the sites were affected by spills of various types of oil. The sixth site was exposed to the effluent from an intertidal heavy metals mine. Table 1 lists the sampling sites and gives a brief characterization of each area. Initial estimates for the extent of pollution are given in Table 2.

Each site was sampled once with the exception of Searsport which was sampled quarterly in 1977 and 1978. Clams were dug using a standard clam hoe. All clams excavated were measured for length to the nearest millimeter using vernier calipers. For Searsport, length data for clams setting after the spill were obtained from Dow (1978, Table 2, p. 47) using ring measurements on live clams from the 1971 year class.

To obtain growth rates clams were aged using length-frequency analysis. A single exception was for Goose Cove where shell ring counts were used exclusively to age the clams. For each site the

Table 1. Description of sampling sites.

Area	Pollution Event	Date of Sampling	Hydrocarbon Concentration ¹	Sediment Characteristics
Basset's Island Red Brook Harbor	No. 2 fuel oil spill from Bouchard No. 65, September 1974	5/12/76	11.4	Predominantly clean sand
Wild Harbor North Falmouth, Massachusetts	West Falmouth oil spill No. 2 fuel oil & detergents from Florida, September 1969	5/3/77	47	Clean coarse sand
Long Cove Searsport, Me.	No.2 fuel oil & JP-4 ² jet fuel spill, March 1971	4/15/77	58	Consolidated sand with silt & some gravel & rock
Gleason Cove Perry, Me.	Crude oil & detergents spill from Irving Oil Refinery, June 1974	8/15/78	11	Consolidated coarse sand and mud with rocks in a patchy distribution
Janvrin Lagoon Madame Island Chedabucto Bay, Nova Scotia	Chedabucto Bay oil spill Bunker C oil from the Arrow, February 1970	7/18/78	38	Muddy sand with some rocks
Goose Cove Harborside, Me.	Effluent from a settling pond of a heavy metals mine, 1969-1972	7/20/76	--	Coarse sand to very consoli- dated sand with rock & shell in a patchy distribution

¹All hydrocarbon concentrations are for the sediment ($\mu\text{g/g}$ dry weight by GC). Samples were taken at the time of clam collection.
Source: C. Brown (personal communication).

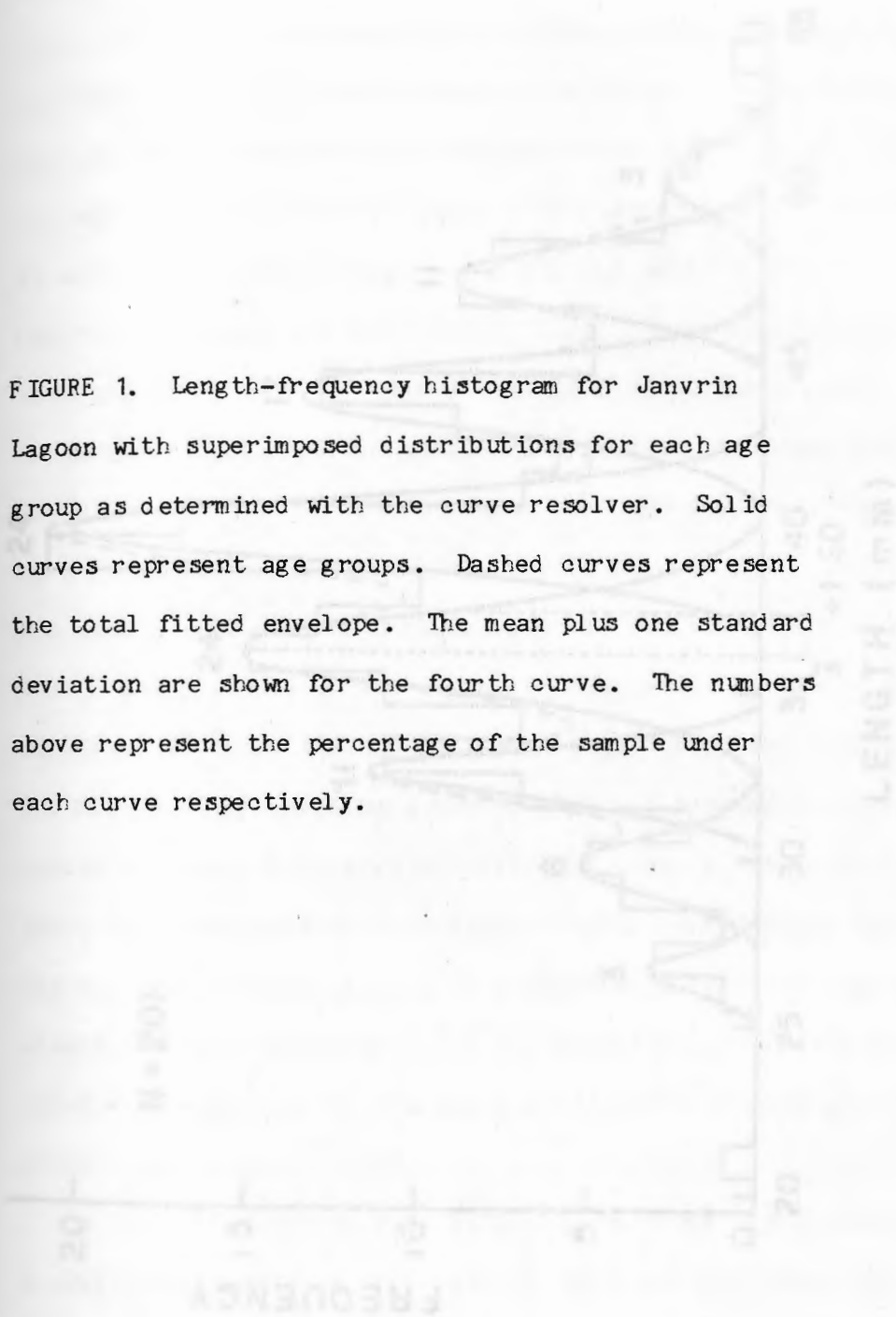
²Originally reported as JP-5 (Gilfillan *et al.*, 1977).

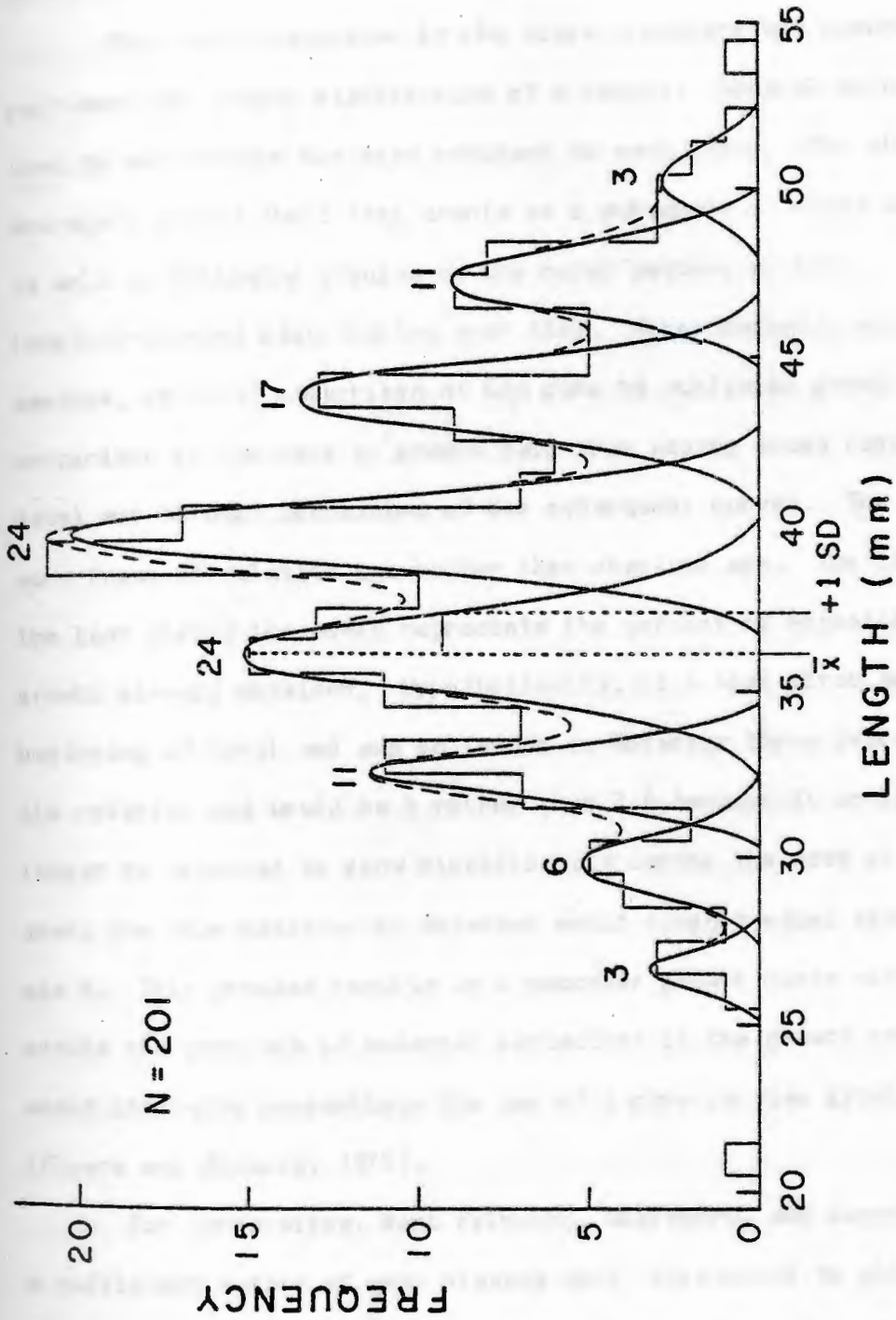
Table 2. The magnitude of pollution at each site.

Area	Pollution History
Bourne	The site was initially covered by oil. Changing wind and current patterns eventually washed most of the oil out of the area. Hampson & Moul (1977) reported that some of the oil was still present in certain marsh areas, but little evidence of oil was found at sampling.
Wild Harbor (West Falmouth)	A sediment concentration of 590 $\mu\text{g/g}$ (dry wt.) was reported at Site II of the WHOI studies. This site is located up a tidal creek (Wild Harbor River) just below the present sampling location. Later concentrations steadily declined reaching 1/3 of the initial value after 2 years (Sanders, 1970).
Long Cove Searsport	The site, located near the inner most of 3 main culverts where oil entered the cove, is equivalent to Station 12 of Mayo <i>et al.</i> (1975) who found an initial concentration of 58 $\mu\text{g/g}$ (dry wt.). At two adjacent stations (11 and 13) sampled the following year the concentration had increased by an order of magnitude. Further contamination was due to oil leaching from saturated sediments upslope.
Perry	Crude oil and detergents initially covered the flat. Little evidence of contamination was found at sampling.
Janvrin Lagoon	The lagoon was initially covered by 30 cm of oil. Much of the oil has remained and is periodically remobilized. Measurements taken 6 years later by Thomas (1978) and Gilfillan & Vandermeulen (1978) showed average concentrations at thousands of $\mu\text{g/g}$ (dry wt.). However, these measurements tended to vary by four orders of magnitude. At sampling oil was still abundant, and a slick would form on any depression made on the flat.
Goose Cove	During mine operations record levels of 8 metals (Mn 341, Cd 1.7, Cr 29.5, Ni 4.1, Zn 195, Pb 55, Fe 2471, Co 1.5 ppm) and extremely high Cu levels were found in soft clams near the outflow. Levels typically ranged 1 to 2 orders of magnitude above those found in control clams (Dow & Hurst, 1972).

length-frequencies were plotted at 1 mm intervals and the modes on the resulting graph were broken down into a series of normal curves by inspection (Peterson Method) (Tesch, 1971; Macdonald and Pitcher, 1979) using a Dupont 310 Curve Resolver. The curve resolver is an analog computer which allows the investigator to break down a complex envelope into its basic components (in this case normal curves) in a graphical fashion. It utilizes function generator channels (10) capable of generating normal curves on a cathode ray tube. The images are then projected on to the length-frequency histogram drawn for each population. The histogram is broken down from left to right (young to old) in the following manner. One channel is switched on and the projected curve is positioned such that its location, width, and height correspond to the left edge of the histogram. The remainder of the histogram is then resolved by successively turning on the channels and positioning them such that the envelope projected (formed by the summation of the outputs of all the 'on' channels) matched the outline of the histogram. The optical output gives the observer immediate feedback, and repeated trials can be made quickly by varying the size, shape, position, and number of curves until it is felt that a reasonable 'fit' to the data has been obtained. At this point the output of each channel can be turned on and displayed independently, and its projection can be traced on the histogram. The result of this process is exemplified in Figure 1. From the resulting graphs the mean and standard deviation of each distribution can be obtained (Macdonald and Pitcher, 1979). The mean occurs at the peak and the standard deviation is the half width at 61% of the height (See curve 4, Figure 1). The curve resolver is also equipped

FIGURE 1. Length-frequency histogram for Janvrin Lagoon with superimposed distributions for each age group as determined with the curve resolver. Solid curves represent age groups. Dashed curves represent the total fitted envelope. The mean plus one standard deviation are shown for the fourth curve. The numbers above represent the percentage of the sample under each curve respectively.





with an integrator which allows one to obtain the percentage of the whole sample under each component curve.

Each curve generated by the above procedure was assumed to represent the length distribution of a cohort. Several methods were used to corroborate the ages assigned to each group. For the Searsport sample shell ring counts on a subsample of clams were used as well as following changes in the modal pattern of the length-frequency distribution over time. Other methods, used for all samples, included comparison of the data to published growth data, comparison of the data to growth data from nearby areas (unpublished data) and through inspection of the subsequent curves. The ages used were those of relative age rather than absolute age. The time beyond the last yearly increment represents the percent of expected yearly growth already obtained. Hypothetically, if a clam first set in the beginning of April and was collected in November three years later its relative age would be 4 rather than 3.6 because it would no longer be expected to grow significantly during the rest of its third year; the size obtained by November would roughly equal its size at age 4. This process results in a smoother growth curve since it avoids the problems of seasonal variations in the growth rate which would otherwise necessitate the use of a more complex growth model (Cloern and Nichols, 1978).

For three sites, West Falmouth, Searsport, and Janvrin Lagoon, a sufficient number of year classes were represented to allow a von Bertalanffy growth curve to be fitted to the data. Only post-spill age classes were used to fit the curve which reduced the number of points available for the analysis. The growth curve was fitted by

nonlinear regression according to Gallucci and Quinn (1979) using the NLIN procedure of SAS 76 (Barr et al., 1976). This procedure yielded estimates of the parameters for the von Bertalanffy growth equation $L = L_{\max}(1 - \exp(-K(t - t_0)))$ where t = time, L = length at time t , L_{\max} = maximum asymptotic length, K = growth constant, and t_0 = time when $L = 0$.

Using the calculated von Bertalanffy curve the growth rate prior to pollution was estimated. This analysis was based on the assumption that growth follows a fixed schedule or pattern. Growth prior to pollution may be different (i.e. have its own growth schedule) from growth after pollution. It was assumed that the post-pollution growth schedule was adequately modeled by the calculated von Bertalanffy curve. The pre-pollution growth schedule was then approximated in the following manner. The length (L_1) of the last year class to set prior to pollution was found. Then the age corresponding to this length on the von Bertalanffy curve was determined. One year was subtracted from this age and its corresponding length (L_2) on the growth curve was determined. Next the length (L_3) corresponding to an age equal to (age at L_1) - 1 was found. The difference between L_2 and L_3 represents the extra growth experienced by clams having one year's growth on the pre-pollution growth schedule. This difference was then added to the expected length at year one on the post-pollution curve (von Bertalanffy curve) to obtain the expected length at year one on the pre-pollution curve. The second point on the pre-pollution schedule was found by applying the above procedure to the year class that set two years prior to pollution. This process was repeated for all available

pre-pollution year classes. An approximation of this technique could be used when few post-pollution points exist by drawing an approximate growth curve by eye. However, it is felt that the variability introduced would reduce the meaningfulness of the results and no such approximations are attempted here.

RESULTS

For each area the mean length and standard deviation for each age group as obtained from the length-frequency analysis are shown in Table 3. These data are plotted in Figures 2-7. For West Falmouth, Searsport, and Janvrin Lagoon the calculated von Bertalanffy curve is also plotted. Table 4 describes the parameters for these curves. In addition, pre-pollution growth approximations for Searsport and Janvrin Lagoon are plotted. For the remaining three areas approximate curves have been drawn by eye to smooth out the age-length relationship and to accentuate its change following a pollution event.

The figures demonstrate that changes in the incidence of pollution are reflected by changes in the growth rate. Only West Falmouth fails to show a significant change. The breaks in the curves clearly indicate that pollution has an adverse effect on growth and they reflect the degree to which growth can be reduced. Growth was severely affected at Searsport, Janvrin Lagoon, and Goose Cove. At Goose Cove growth improved following pollution abatement. At West Falmouth the lengths of the year classes existing prior to the spill fail to differ significantly from the lengths expected on the basis of post-spill growth. It would appear that the spill had

Table 3. The age (yrs.), length (mm), standard deviation, and percent of the sample population for each year class at each site as determined by length-frequency analysis. The sample size for each site is given in parentheses.

Age	Length	% of Sample	Age	Length	% of Sample	Age	Length	% of Sample
Bourne (187)			Goose Cove (101)¹			Searsport (152)²		
1.15	22.7 (2.2)	8	3	24.1 (1.9)	7	1	10.0 (3.0)	
2.15	30.6 (2.4)	5	4	34.3 (3.8)	12	2	18.3 (3.7)	
3.15	40.8 (2.4)	14	5	36.4 (4.1)	25	3	24.9 (3.7)	
4.15	48.2 (2.3)	27	6	39.6 (3.2)	23	4	31.1 (4.2)	
5.15	54.4 (1.3)	10	7	46.6 (9.8)	5	5	34.4 (4.5)	
6.15	58.9 (1.5)	9	8	47.7 (17.2)	17	6.2	38.0 (0.6)	2
7.15	64.3 (2.1)	12	9	55.2 (6.9)	6	7.2	41.5 (1.4)	3
8.15	70.5 (1.3)	8	10	61.5 (2.1)	2	8.2	44.9 (1.0)	6
9.15	75.7 (2.0)	3	11	59.5 (5.8)	4	9.2	47.2 (0.6)	5
West Falmouth (183)			Janvrin Lagoon (201)					
1.15	28.6 (2.6)	9	3.5	21.0	0.5	10.2	49.9 (1.0)	14
2.15	38.8 (2.6)	3	4.5	26.7 (0.7)	3	11.2	53.0 (1.2)	15
3.15	45.2 (1.5)	2	5.5	29.9 (0.9)	6	12.2	55.3 (0.7)	11
4.15	53.3 (2.9)	27	6.5	32.6 (0.8)	11	13.2	57.0 (0.8)	10
5.15	61.6 (1.5)	8	7.5	36.2 (1.3)	24	14.2	59.0 (0.9)	18
6.15	68.2 (1.9)	20	8.5	39.7 (1.0)	24	Perry (180)		
7.15	73.4 (1.7)	7	9.5	43.8 (1.0)	17	3.67	36.4 (1.5)	3
8.15	78.8 (1.4)	5	10.5	47.4 (1.0)	11	4.67	41.1 (1.5)	11
9.15	84.5 (2.6)	1	11.5	50.3 (1.0)	3	5.67	47.1 (1.8)	29
			12.5	54.0	0.5	6.67	55.2 (2.3)	46
						7.67	62.3 (0.8)	5
						8.67	66.9 (0.8)	3
						9.67	70.9 (1.9)	3

¹Ages determined by counting shell rings

²First five year classes from Dow (1978)

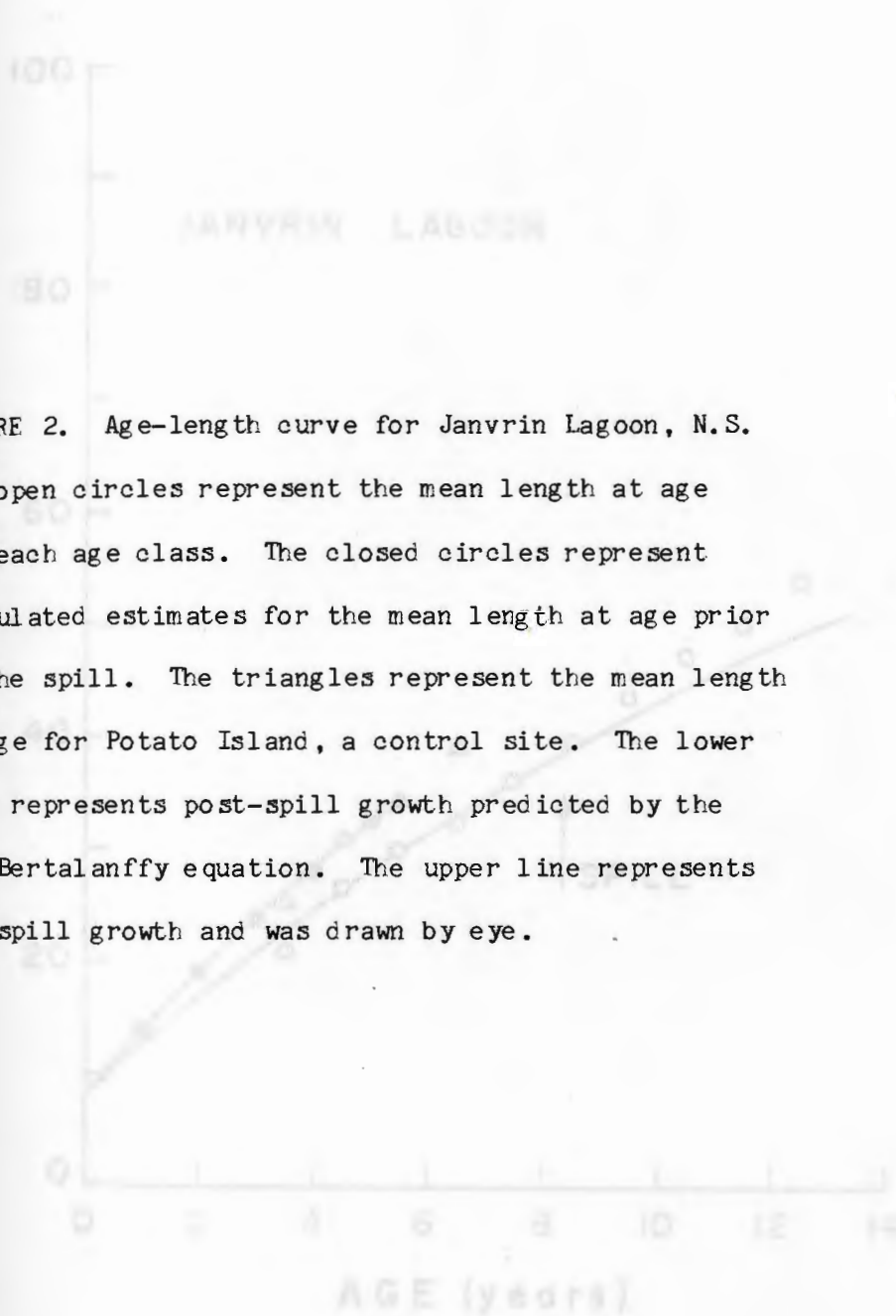
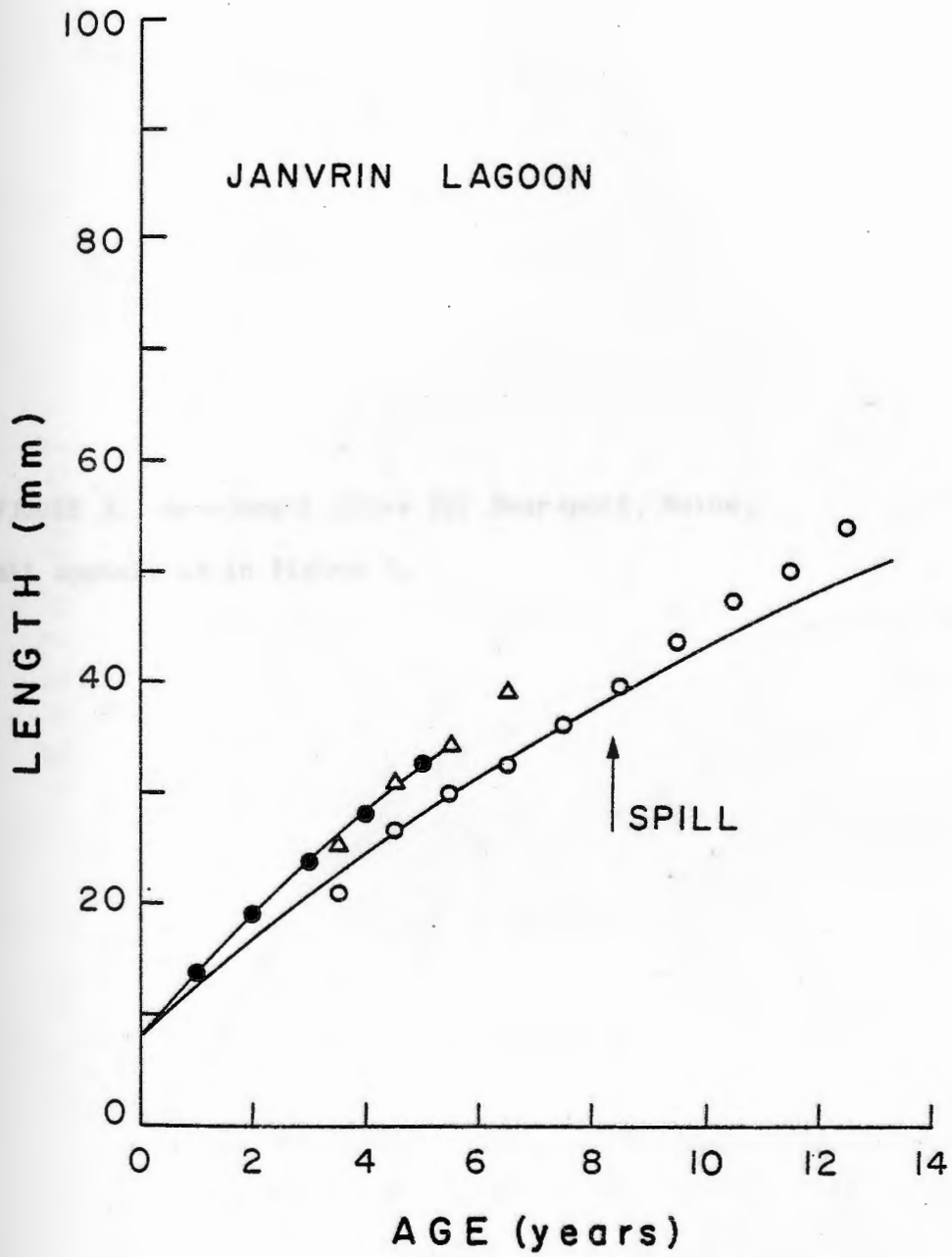


FIGURE 2. Age-length curve for Janvrin Lagoon, N.S.

The open circles represent the mean length at age for each age class. The closed circles represent calculated estimates for the mean length at age prior to the spill. The triangles represent the mean length at age for Potato Island, a control site. The lower line represents post-spill growth predicted by the von Bertalanffy equation. The upper line represents pre-spill growth and was drawn by eye.



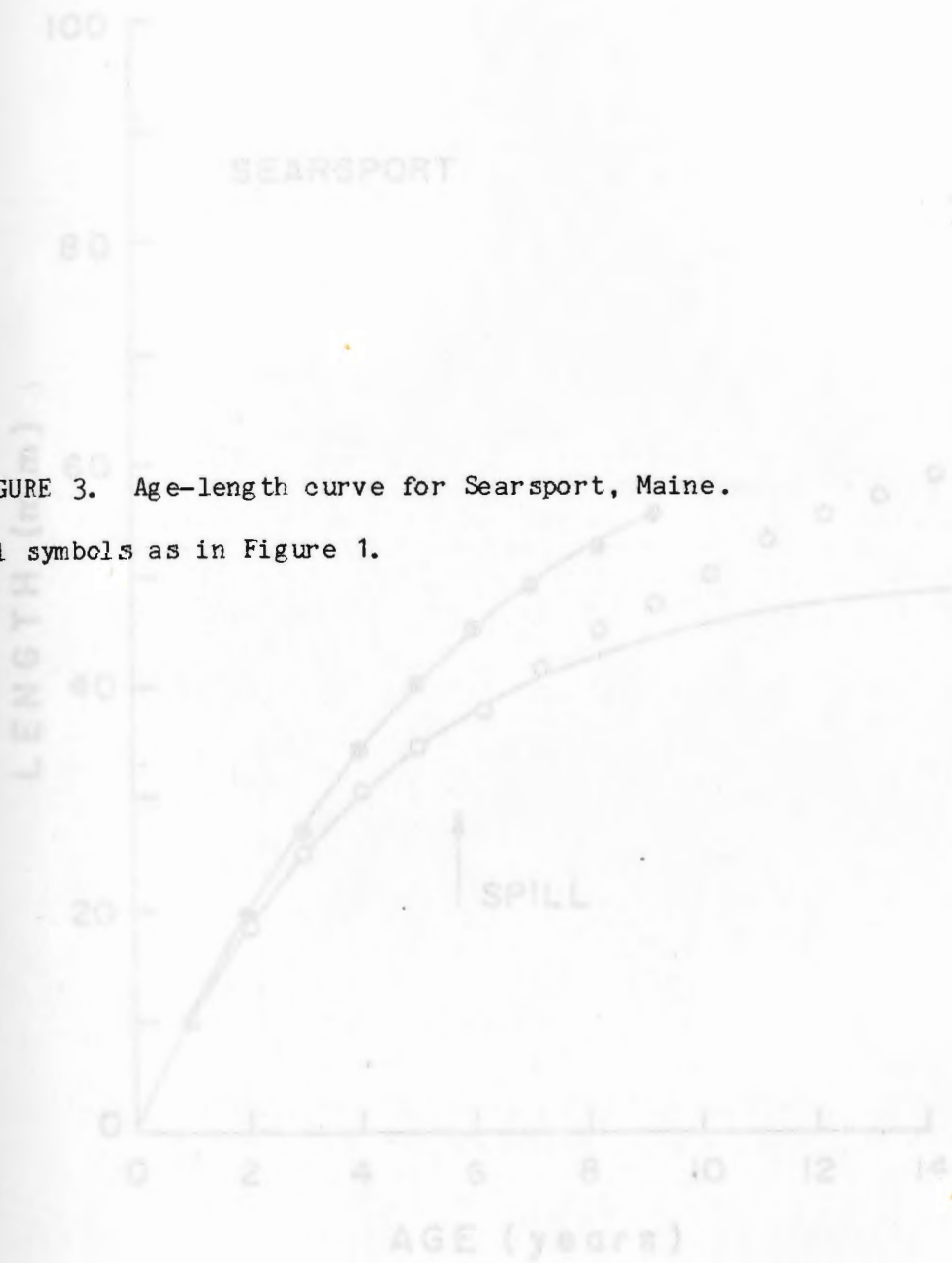
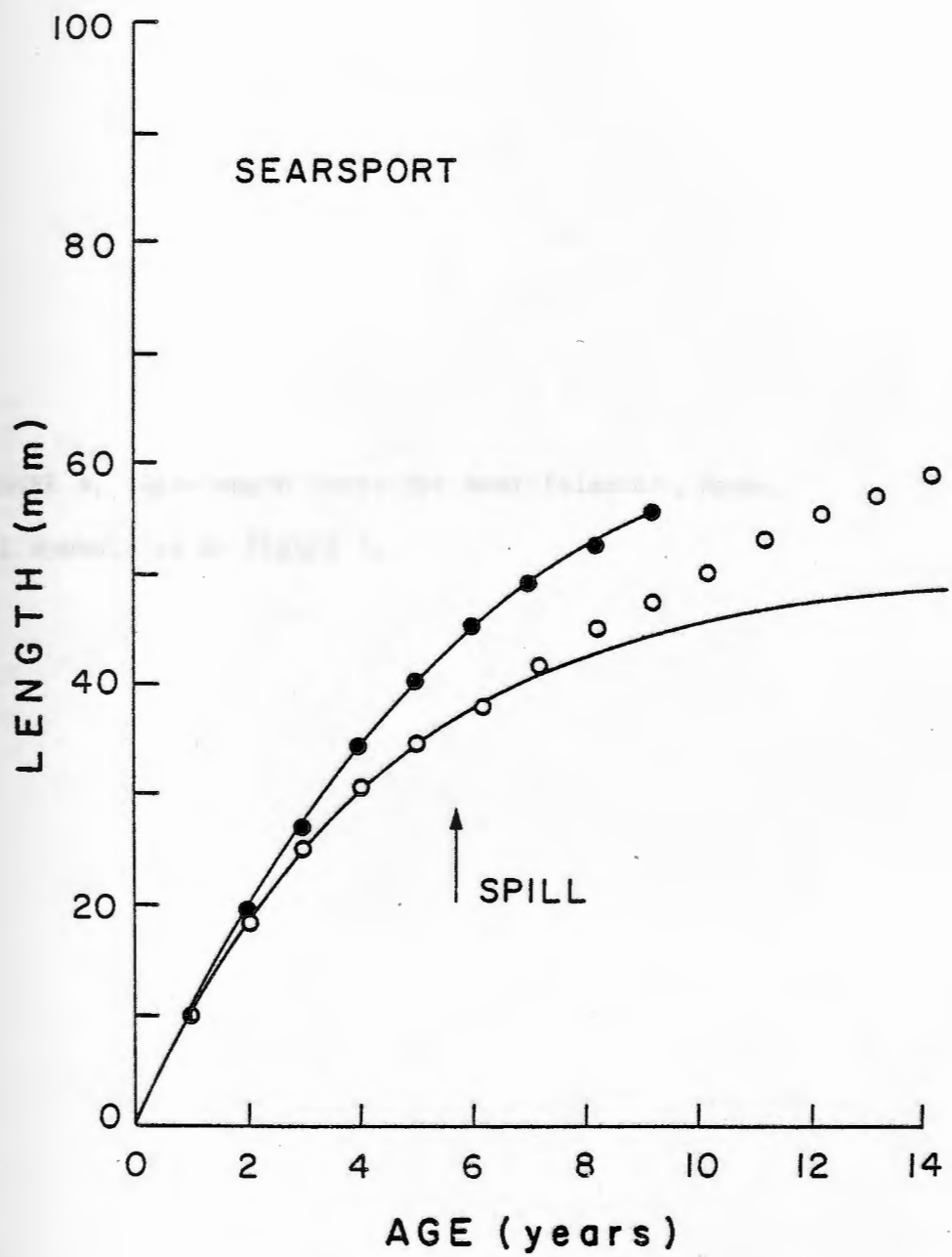


FIGURE 3. Age-length curve for Searsport, Maine.

All symbols as in Figure 1.



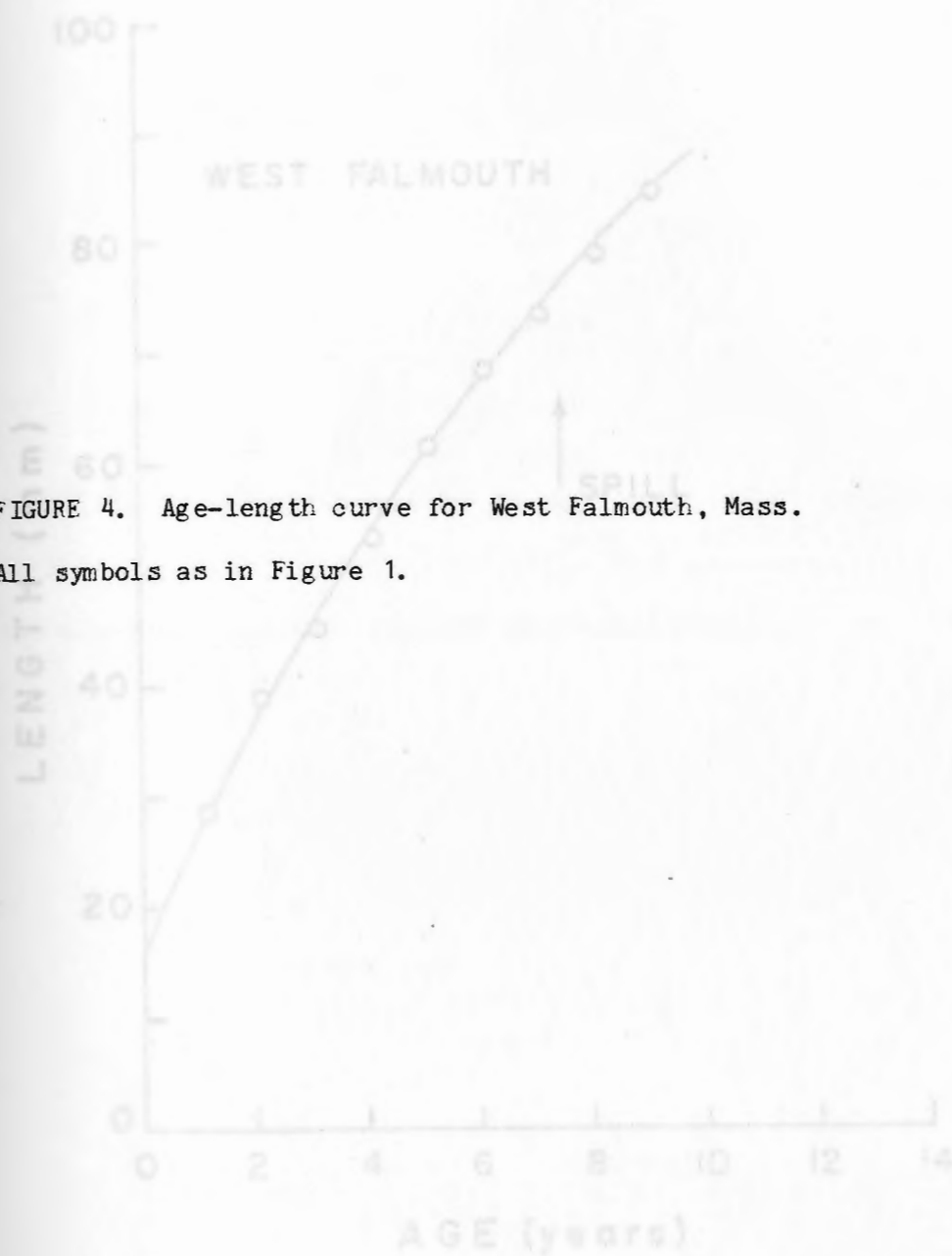
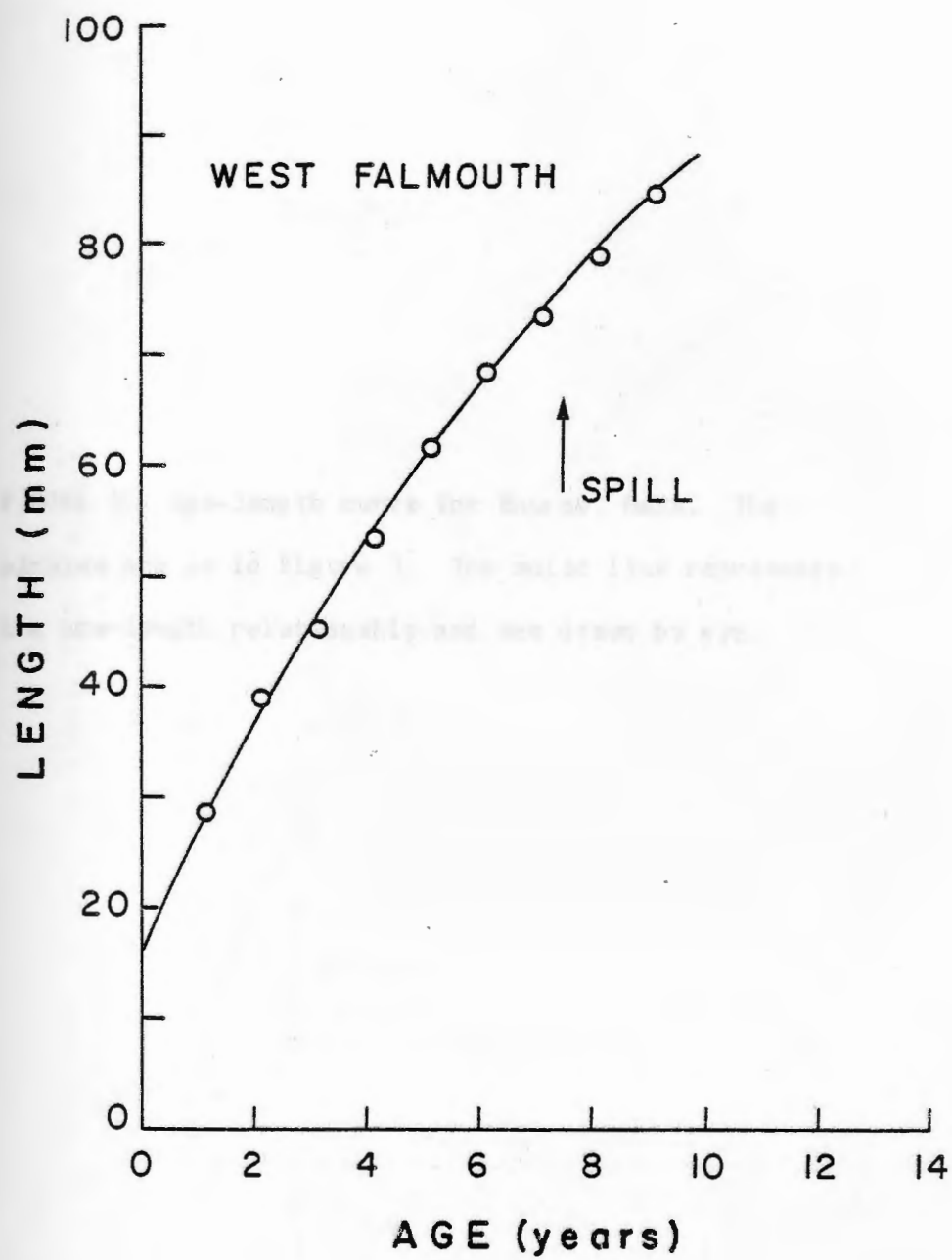


FIGURE 4. Age-length curve for West Falmouth, Mass.

All symbols as in Figure 1.



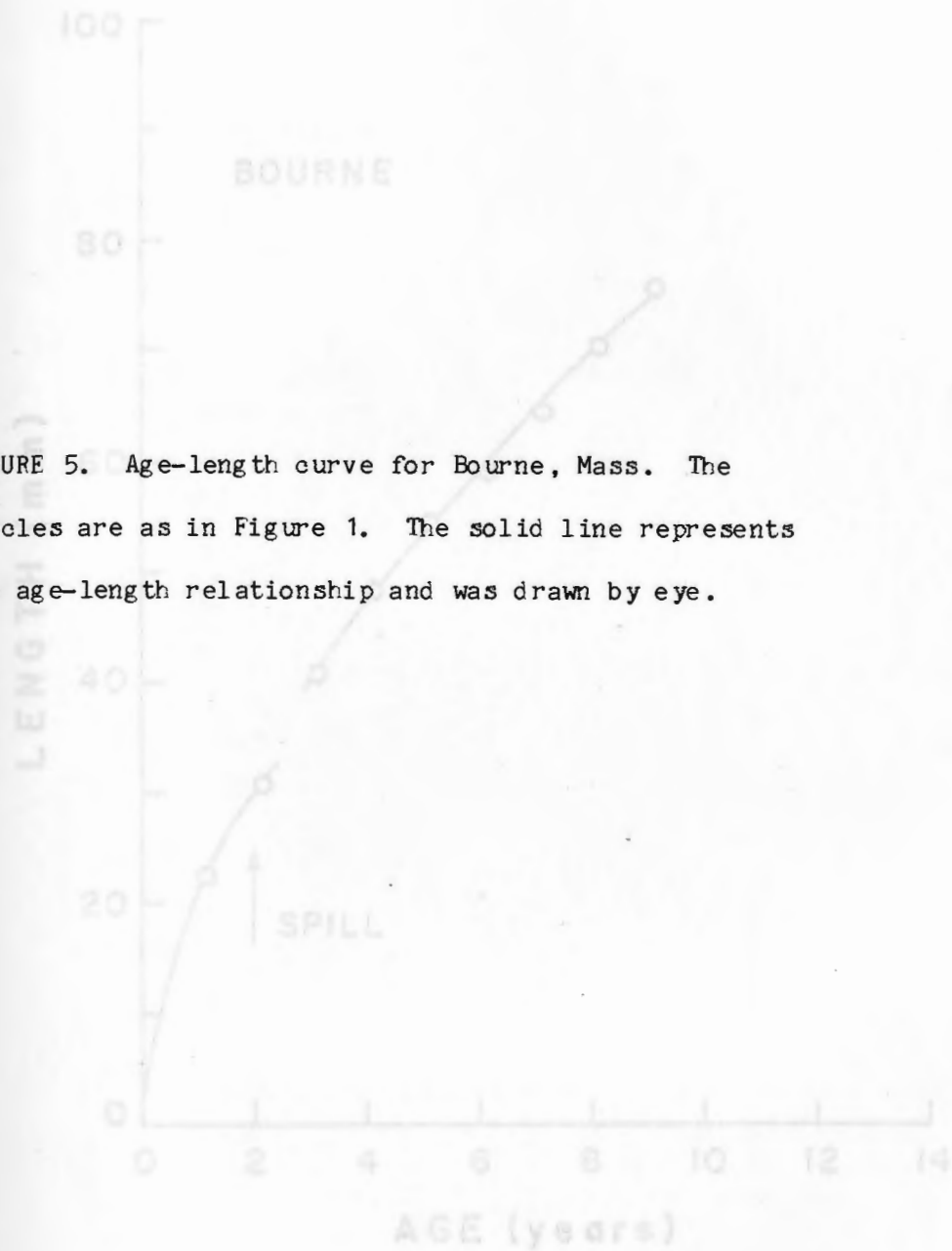
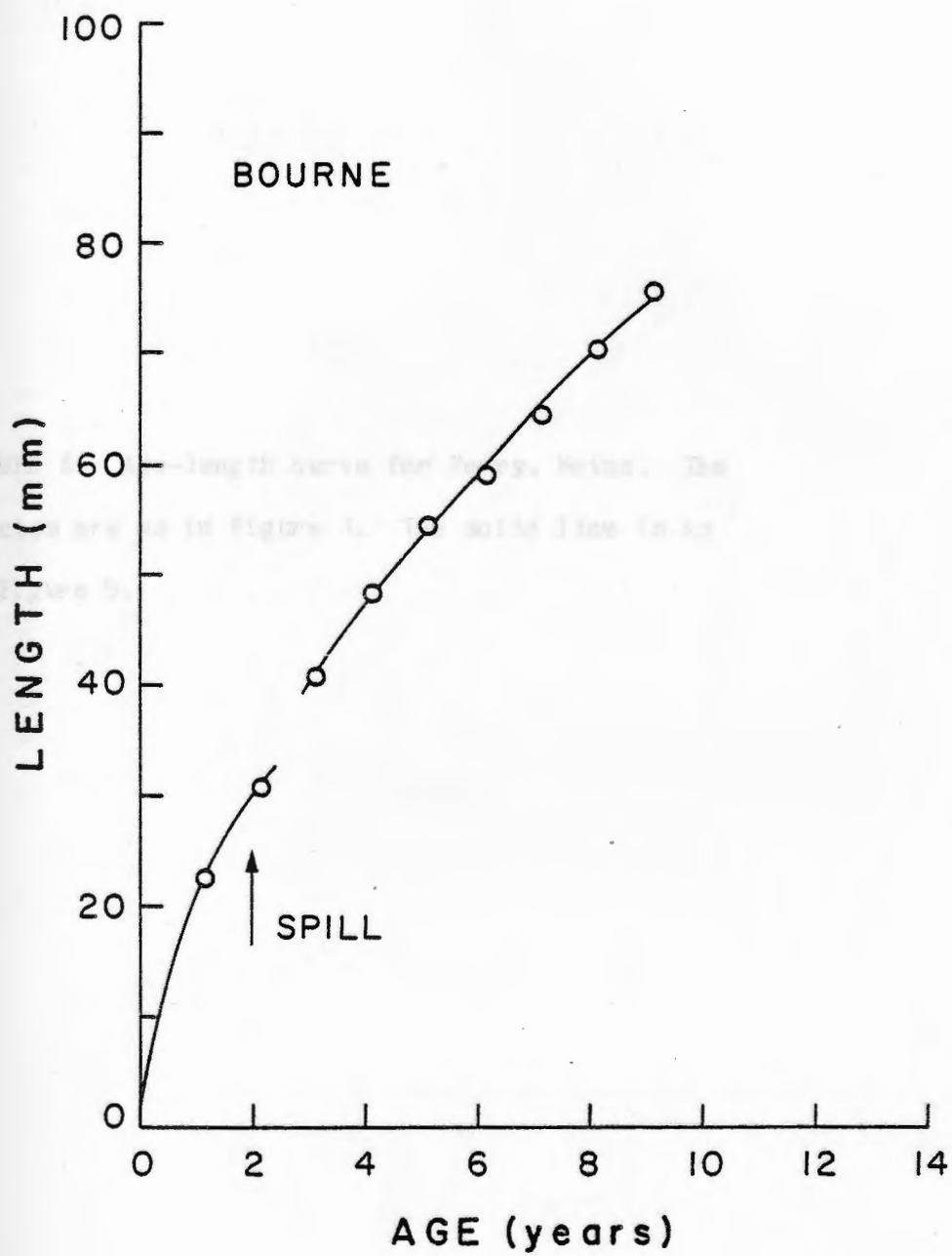


FIGURE 5. Age-length curve for Bourne, Mass. The circles are as in Figure 1. The solid line represents the age-length relationship and was drawn by eye.



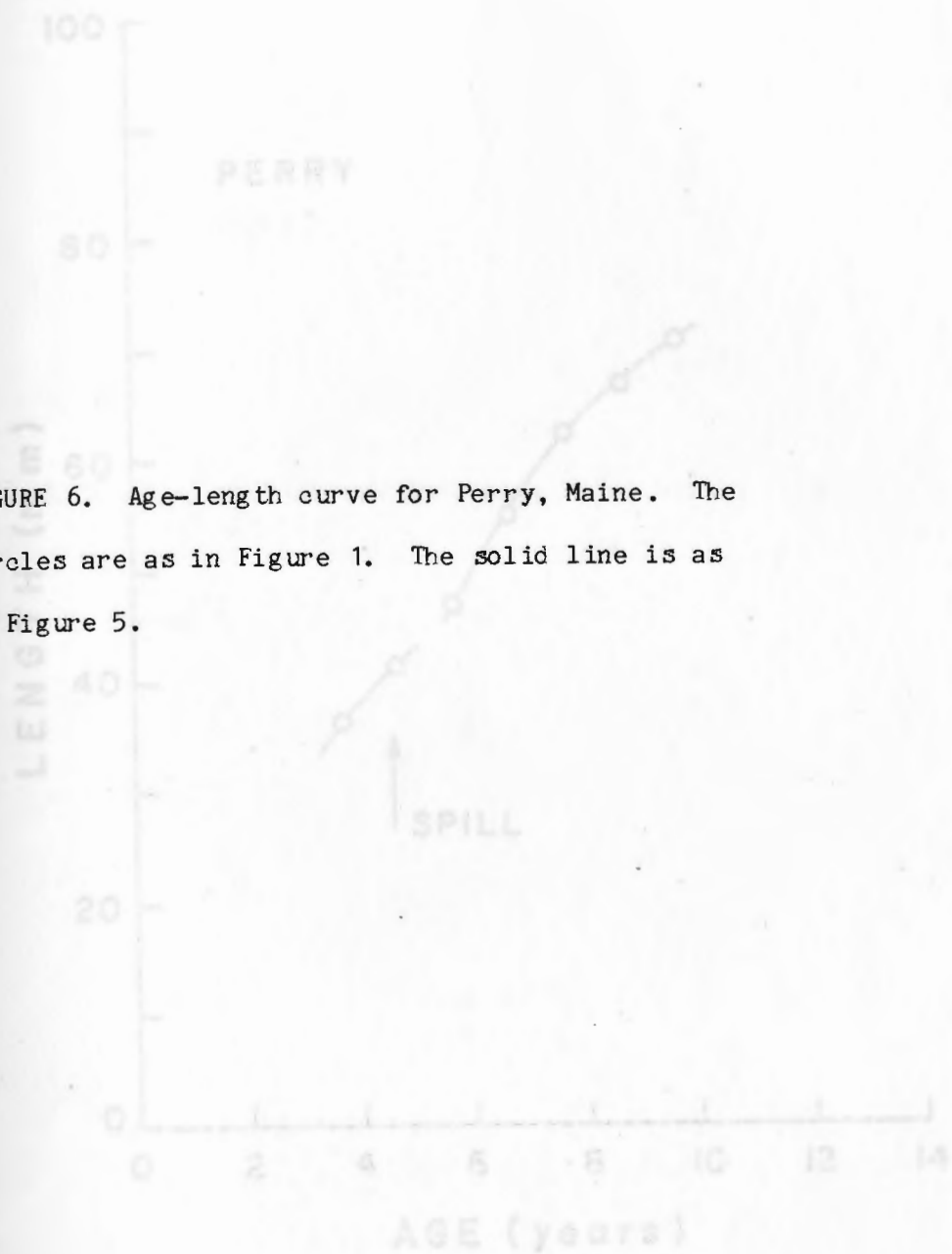
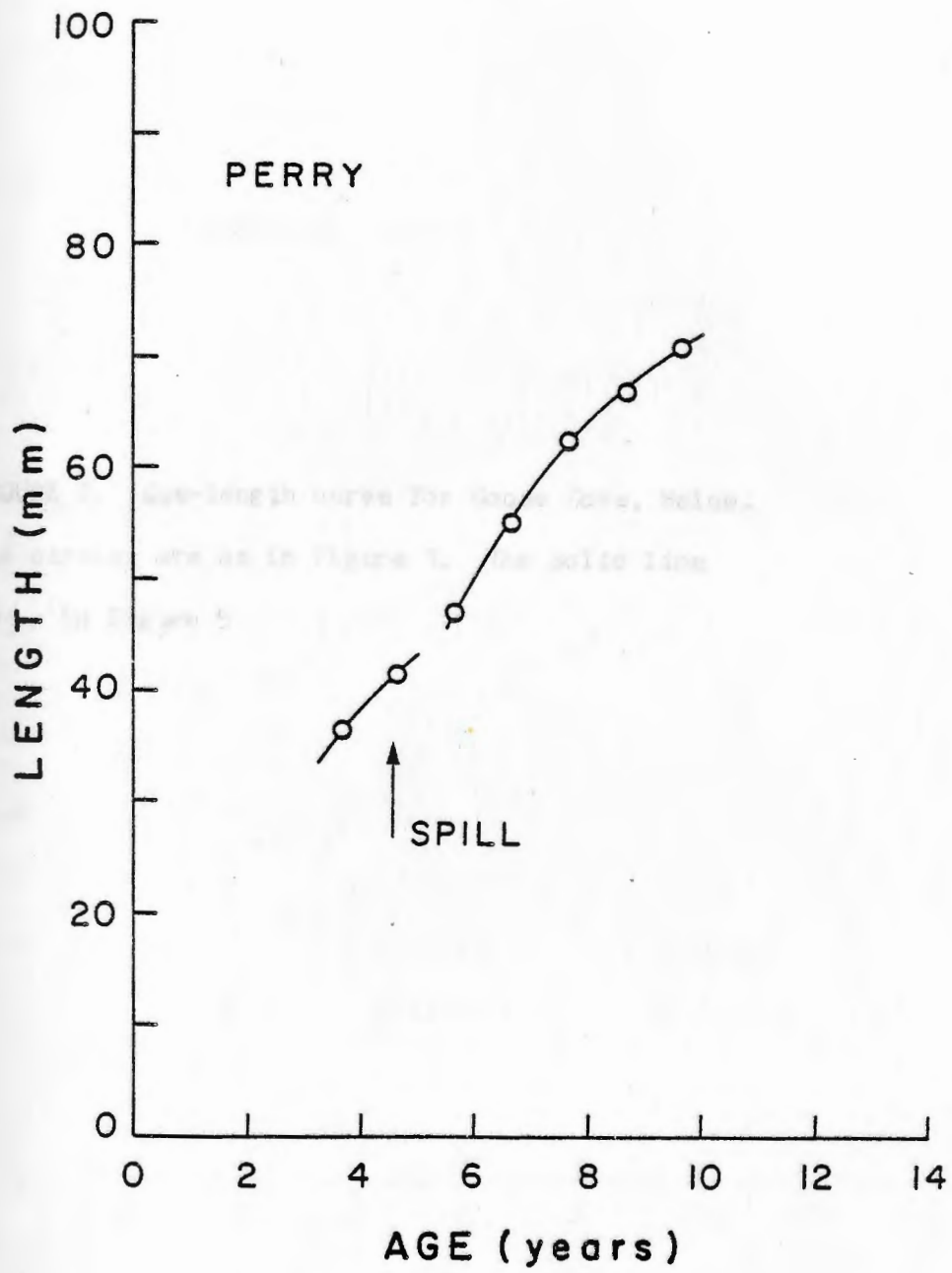
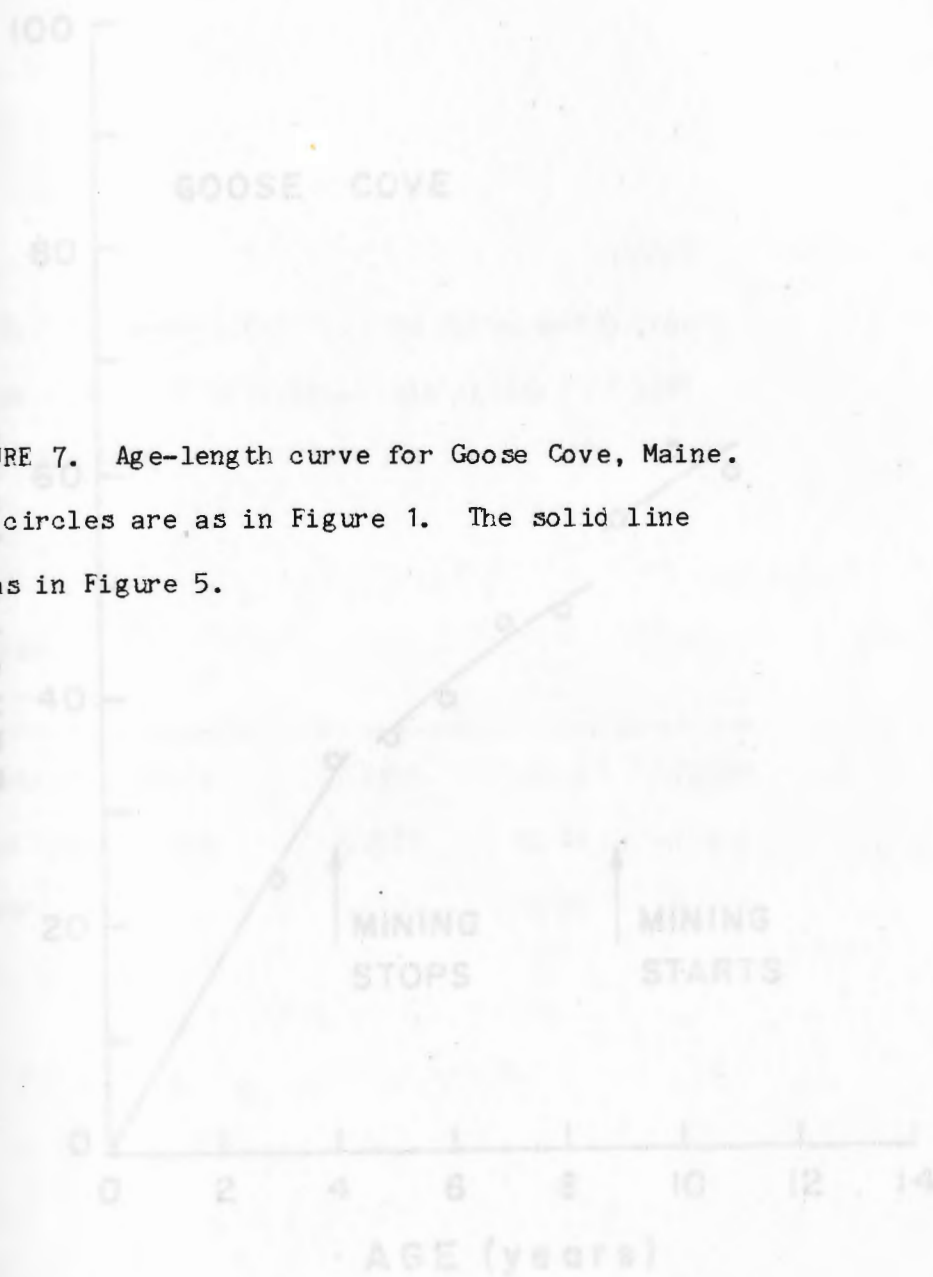


FIGURE 6. Age-length curve for Perry, Maine. The circles are as in Figure 1. The solid line is as in Figure 5.





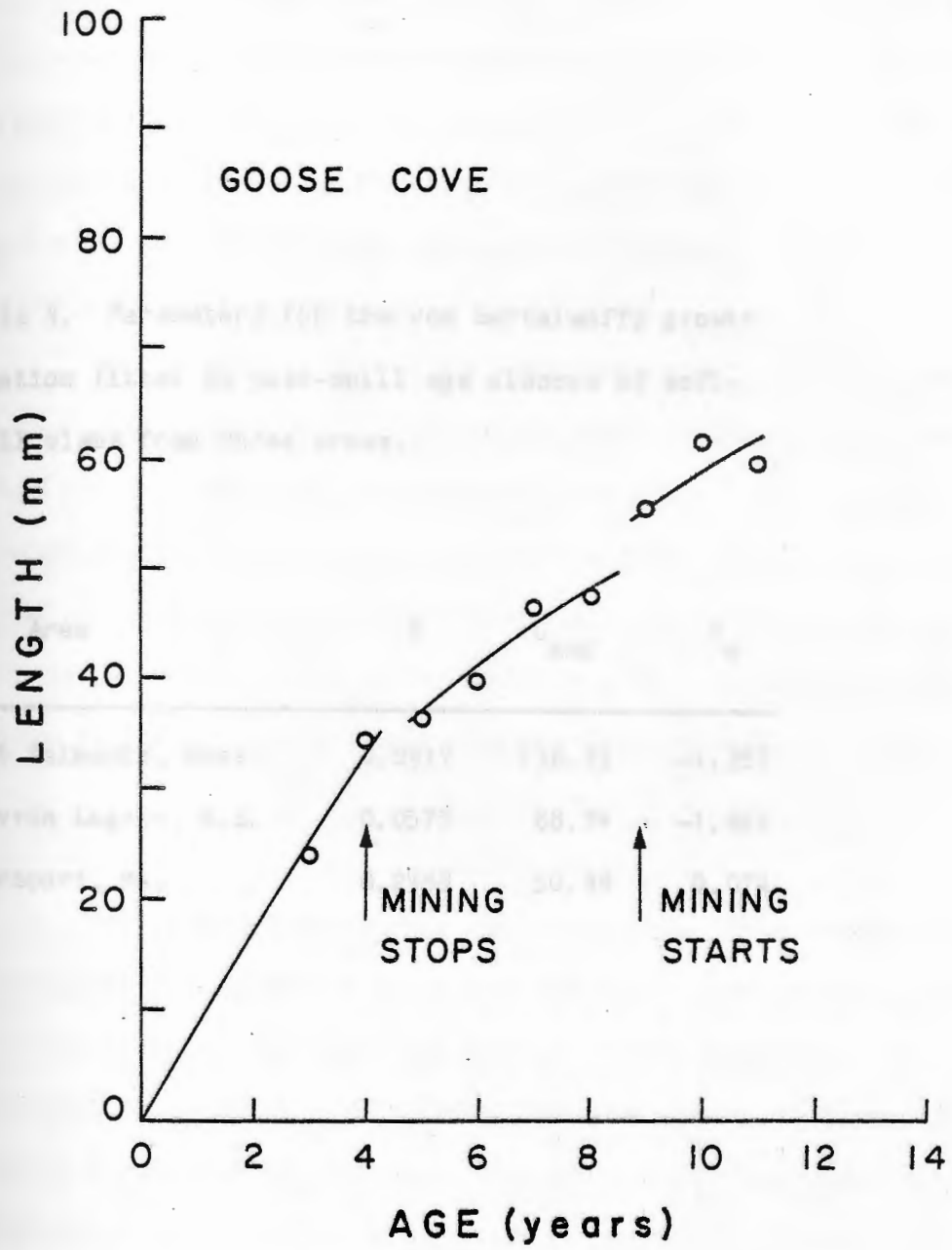


Table 4. Parameters for the von Bertalanffy growth equation fitted to post-spill age classes of soft-shell clams from three areas.

Area	K	L_{max}	t_0
West Falmouth, Mass.	0.0917	136.73	-1.357
Janvrin Lagoon, N.S.	0.0575	88.74	-1.622
Searsport, Me.	0.2358	50.48	0.074

no drastic effect on growth in clams from the collection site.

For comparison purposes the age-length determinations for Potato Island (unpublished data) are plotted in Figure 2. This area was used as a control site by Thomas (1978) and by Gilfillan and Vandermeulen (1978) in their studies of Chedabucto Bay. In the latter study it was reported that soft clam growth at Janvrin Lagoon and Potato Island were similar prior to the spill. The estimate of pre-spill growth calculated here agrees remarkably well with the age-length determinations for Potato Island.

The parameters of the von Bertalanffy curve for Searsport appear anomolous in comparison to the other values shown in Table 4. This probably resulted from sampling errors (note the standard deviations in Table 3) associated with a small sample size ($N=15$) and from successive improvements in post-spill growing conditions (see discussion below). The latter would tend to increase the initial slope of the age-length curve, thereby increasing K .

DISCUSSION

The problems inherently associated with the estimation of population age structure and growth through length-frequency analysis were reviewed by Macdonald and Pitcher (1979) and others. A reiteration of these problems does not seem necessary here. It should be pointed out, however, that the growth being measured is that for a cohort of the population and not of individuals (see Ricker, 1975; pp 217-218). The difference between the two arises from the fact that the older modes in the length-frequency histogram are usually composed of slower growing individuals. It has been

shown for fish that individuals which grow rapidly tend to mature earlier, become senile earlier, and die earlier than slow growing individuals (Gerking, 1957). For M. arenaria in general an inverse relationship has been found between longevity and the rate of growth (Newcombe, 1936), i.e. older clams are slow growers. A good example of this has been shown by Dow (1978) for clams growing at Searsport. As clams grow their burrow depth increases. Faster growing clams were penetrating the buried stratum of oil polluted sediment at an earlier age whereupon mortality occurred. Hence only the slower growing individuals survived and they now constitute the bulk of the older age groups in the population.

The assumption that clams grow according to a fixed schedule (especially after a pollution incident) is probably not valid. For example Dow (1978) has shown successive improvements in the growth of M. arenaria for each year class following the Searsport oil spill. This is due both to the further weathering of the oil and through the further deposition of clean sediment over the oil contaminated sediment. However, at Searsport and Janvrin Lagoon post-spill recovery has been slow enough to allow the use of the von Bertalanffy curve to generate pre-spill growth estimates. Since only approximate growth estimates have been obtained no effort was made to apply rigorous statistical analysis to the data. It is sufficient here only to illustrate the apparent gross responses of population growth.

The results of this study show that there is a response in the growth rate to environmental changes due to pollution. This response is characterized by a noticeable break in the age-length curve. In each case the onset of pollution was coupled with a reduction in

growth. The exact mechanisms for the observed growth reductions at each site are unknown. The volume of literature on the effects of pollutants on marine organisms in general and on bivalves in particular is now vast but it is still difficult to relate specific effects in the laboratory to responses observed in the field.

For M. arenaria other field studies have shown that the onset of oil pollution is generally followed by a reduction in growth and an increase in mortality. Dow (1975) found a 65% reduction in the annual growth rate of clams transplanted to a site polluted with Iranian crude oil. At Searsport he reported a reduction in the growth of soft clams following the spill (Dow, 1978). That mortality at Searsport greatly increased when clams came into direct contact with the oil seems to indicate the the oil has either a direct toxic effect or that it leads to smothering (Dow and Hurst, 1975; Dow 1978). Smothering was considered to be the main cause of the large soft clam mortality following the spill of Bunker C oil at Chedabucto Bay (Thomas, 1973). Gilfillan and Vandermeulen (1978) found a reduced carbon flux in soft clams from Janvrin Lagoon as compared to Potato Island. This was coupled with a calculated reduction in the rate of shell growth in Janvrin Lagoon clams following the spill. In an earlier study Gilfillan et al. (1975) found a 50% reduction in the carbon flux of soft clams polluted by No. 6 fuel oil. They concluded that for bivalves a reduction in the assimilation ratio was a general response to environmental stress which could be triggered by a number of factors including pollution.

For West Falmouth the age-length curve failed to show a break at the time of the spill. There are two possible explanations for

this. The first explanation is sampling error. Because sampling took place 8 years after the spill it is possible that the age of the sample masked any true effect. Only 6% of the sample consisted of clams that had set prior to the spill. Such a small sample size could have led to underestimation of the mean lengths for each age class.

The second explanation is that the curve accurately reflects the spill's true effect on growth. While this may be true studies made after the spill indicated initially severe effects. Blumer et al. (1970) reported large mortalities among the benthos, including shellfish, immediately following the spill. Site II was particularly devastated (Sanders, 1978). A hydrocarbon concentration of 69 $\mu\text{g/g}$ (dry wt.) was found in oysters from the tidal creek (Blumer et al., 1970) one month after the spill. This value is above those reported for soft clams from other oil impacted sites (Brown et al., 1979). It seems unlikely, then, that clam growth would have remained unaffected. If conditions improved, however, the effect might become unnoticeable. Sediment oil concentrations at Site II steadily decreased over time reaching 140 $\mu\text{g/g}$ after two years. This is only twice the level reported for indigenous sedimentary hydrocarbons within the area (Blumer and Sass, 1972). The degree of this decrease may be attributable to sediment characteristics at the sampling site. Loose coarse, shifting sand should facilitate rapid depuration or burial of the oil. As a result growth may only have been affected during the first couple of years. Significantly improving conditions invalidate the assumption of a fixed post-spill growth schedule. Hence the von Bertalanffy curve cannot be expected to approximate the

growth of an affected population. Given the sampling problems mentioned above and the 8 year time lag between sampling and the spill any initial effect on growth would now be undetectable by the methods used. This situation differs both from Bourne and Perry, sites where little oil was found but which were sampled shortly after the spill, and from Searsport and Janvrin Lagoon, sites sampled several years after contamination but which still contained enough oil to adversely affect growth.

The mining operations at Goose Cove could have led to a reduction in growth through three mechanisms: siltation, food destruction, and direct heavy metal toxicity. Dow and Hurst (1972) suggested that much of the damage done by the mining operations was due to heavy siltation and smothering. This would definitely interfere with feeding by clogging the clams' filtering apparatus. They also reported that the mine effluent was highly toxic to phytoplankton, the main food source for soft clams, and that this could contribute to malnutrition and starvation. Eisler (1977) reported that M. arenaria was fairly susceptible to heavy metal contamination. Many of the metal concentrations reported by Dow and Hurst (1972) were higher than the lethally toxic concentrations determined in bioassay studies dealing with pure (Eisler and Hennekey, 1977) and mixed (Eisler, 1977) metal solutions.

The concentrations of metals in soft clams at Goose Cove were still high at the time of sampling, four years after mining operations ceased (L. Fink, personal communication). From the graph in Figure 7 it can be seen that growth improved following pollution abatement, although it did not seem to have returned to its original

rate. If starvation and smothering were the major contributing factors to reduced growth then growth should have dramatically improved upon the cessation of mining activities. This may have been the case. However, the exact degree of recovery is difficult to gauge in this case due to the variability of the data. These observations would lead one to conclude that smothering and starvation were major factors working in conjunction with direct toxicity to reduce growth during the period of mining operations. In addition, it appears that to some extent growth was still being adversely affected at the time of sampling possibly due to direct toxic effects.

The pronounced growth reduction at Goose Cove can be attributed to the variety of ways in which the mining effluent affected the clams and to the constant output of effluent during the period of mine operation. Once mining operations ceased recovery was fairly rapid. This is in contrast to recovery at oil polluted sites and reflects the persistence of oil in the sediment, and the different mechanisms by which oil and mining effluent affect clams. Major contributing factors toward reduced growth at Goose Cove such as siltation and food reduction were removed after mining operations ceased. On the other hand, oil itself is a major factor in growth reduction. Oil can be taken up through the siphons (Fong, 1976) and the leaching of oil from saturated sediments following a spill can result in a contaminated water supply for an extended period of time (Mayo et al., 1975). Because oil can be detrimental upon contact (Dow, 1978), the effects of a spill can persist after burial of the oiled sediment. In addition, Vandermeulen (1977) and Vandermeulen

and Penrose (1978) found that significant quantities (40%) of oil remained in polluted soft clams following three month exposure to clean water. All these factors contribute to the persistence of an effect following initial hydrocarbon contamination.

In spite of these tendencies, some areas showed signs of recovery. No break in the age-length curve was observed at West Falmouth as discussed earlier. Bourne seems to be a similar case. Little evidence of oil was found at the time of sampling, and the break in the curve (Figure 5) appears like a short depression in an otherwise normal looking growth curve. This would seem to indicate that growth was disrupted only for a short period of time, on the order of a few years.

The techniques used here are considered valuable in assessing pollution effects. Primarily they are useful in detecting gross responses in growth due to changes in environmental quality and they allow one to estimate pre-pollution growth. This is helpful since measurements taken prior to a pollution event are rare and usually fortuitous. A number of studies have used shell growth bands to monitor, in detail, subtle environmental changes (e.g. Kennish and Olsson, 1975). However, these techniques are limited in their application and the methods are involved and costly. The techniques used here sacrifice detail but have more general applicability. For example they allow one to study populations of M. arenaria south of Cape Cod where annual ring formation is unreliable (Mead and Barnes, 1904; Shuster, 1951). The responses observed only directly reflect the effects on growth. They do not directly reflect changes in mortality, settlement, or population age structure. As was observed

at Searsport, however, continued size-dependent mortality may indirectly affect the resulting growth curve.

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SUMMARY

The relationships between various life-history parameters were studied in the population of the soft-shell clam, *Mya arenaria*, in order to elucidate the species' strategy of adaptation and life-history strategy. The relationships between growth and the other parameters were not considered in the context of life-history strategy in the environment.

ADAPTATIONS TO ENVIRONMENTAL VARIATION AND THE LIFE-HISTORY STRATEGY OF THE SOFT-SHELL CLAM, *Mya arenaria*: Relationships Between Parameters

and the life-history traits: faster growth, greater fecundity, greater longevity, larger size of maturation, longer and more numerous eggs, and decreasing longevity. With the exception of longevity, these relationships are those which in the literature are associated with the predictions of a high-investment life-history strategy. Decreasing longevity can be achieved by the increase in size of the *Mya arenaria*, a larval species, during the earlier portions of its reproductive range. In terms of life-history evolution high and exclusive density independent juvenile mortality is seen to be a more important factor than a trend to high mortality.

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This trend seems to be associated with the condition of the organism and perhaps a physiological response to high mortality which may be caused by genetic selection in the population which is the environment.

The population of *Mya arenaria* was found to be significantly greater than the population of *Mya*. An increase in a population would also increase the density, and the high density would...

SUMMARY

Relationships between various life-history parameters were studied in 25 populations of the soft-shell clam, Mya arenaria, in order to elucidate the species's modes of adaptation and life-history strategy. The relationships between growth and the other parameters were analyzed within the context of latitudinal variations in the environment. An association was found between decreasing latitude and the following traits: faster growth, greater variations in juvenile mortality, larger size of maturation, larger egg size, lower egg density, and decreasing longevity. With the exception of longevity, these relationships and those evident in the literature are consistent with the predictions of a bet-hedging life-history strategy. Decreasing longevity can be explained by the increase in stress on M. arenaria, a boreal species, toward the southern portions of its geographical range. In terms of life-history evolution high and variable density independent juvenile mortality is seen to be a more significant factor than a trend in adult mortality.

Pair-wise comparisons between populations on a local scale showed a relationship between larger egg size and greater egg density. This trend seems to be associated with the condition of the population and represents a physiological response to local conditions within the framework imposed by genetic adaptations to latitudinal variations in the environment.

The proportion of females (52%) was found to be significantly greater than the proportion of males. No evidence of a mechanism behind this disparity was detected, and its cause remains enigmatic.

INTRODUCTION

The theory of life-history strategies has developed rapidly over the last 15 years. A life-history strategy is a design for survival. It consists of a set of traits coadapted through natural selection, which provide a species with a means of dealing successfully with environmental problems. In other words, a strategy is the way a species genetically adapts to variations in its environment. Stearns (1976) provided an excellent review of the history and development of the study of life-history tactics. He emphasized the need for more empirical work and suggested that this work be done through the study of intraspecific populations in contrasting environments.

A major factor limiting the number of empirical studies is the difficulty in measuring the necessary population parameters, especially those involving reproduction. As a consequence, only a few studies have been conducted on benthic invertebrates and these have primarily dealt with brooding species. This work is exemplified by an excellent study on the freshwater mussel Anodonta piscinalis by Haukioja and Hakala (1979). Much less work has been done on broadcast spawners. Age-fecundity relationships have been reported for the mussel Mytilus edulis (Thompson, 1979; Bayne, 1976) and for the soft-shell clam Mya arenaria (Brouseau, 1978b). Further work on the fecundity and mortality schedules of Mya arenaria has been attempted (Brouseau, 1978a).

Mya arenaria is a suitable species for the study of life-history strategies. It is abundant and occupies a variety of habitats over a wide geographic range. Thus Mya encounters a wide

range of conditions, and thereby satisfies Stearns's (1976) criterion of contrasting environments. Being a deep burrowing infaunal filter feeder, Mya is exposed to both the conditions of the substrate and the overlying water column. Being sedentary it cannot escape any prolonged deleterious environmental perturbations; to survive it must be able to cope with these problems. Lastly, M. arenaria is commercially important (MacKenzie, 1979) and further understanding of the species may prove useful to its management.

The purpose of this study is to establish relationships between various life-history parameters in Mya arenaria and to use those relationships to elucidate its life-history strategy. The parameters are estimated from data collected on 25 populations of Mya arenaria. These populations were initially sampled for a study on neoplasia and pollution (Brown et al., 1979). As such, the sampling design and the data obtained were not entirely suited for the present study. Samples were collected at different times and under different conditions. Many of the estimates made here are crude approximations and estimates could not be made on all parameters for all populations. This variability makes individual comparisons tenuous. However overall trends can be deduced. It has been shown that a considerable and consistent change in environmental parameters (temperature, tidal position, sediment grain-size distribution) exists with changing latitude (Appeldoorn, 1980). This study deals mainly with the response of Mya arenaria to this latitudinal gradient in its environment.

MATERIALS AND METHODS

Data Collection

Samples of soft-shell clams were collected at 25 sites along the northeast coast of North America (Table 1 and Figure 1). All individuals were measured for shell length, weighed, and sectioned for histological analysis. The sections were prepared using standard histological techniques (Brown et al., 1977), cut at 6 μ m, and stained with hematoxylin and eosin. These data were then analyzed to obtain estimates of some population life-history parameters.

Calculation of the Variation in Juvenile Mortality (VJM)

To adequately discuss variations in population parameters it is necessary to have some estimate of the stability of the various environments. Environmental stability can be inferred by a low variability in reproductive success or juvenile mortality (Stearns, 1976). To estimate the variation in juvenile mortality an adaptation of catch-curve analysis (Ricker, 1975) was employed. Under the assumption of constant adult mortality and nonselective sampling there is a linear relationship between age and the natural logarithm of age-class size. Data from Brouseau (1979a) indicate that adult mortality in M. arenaria is uniformly low among the age classes studied. In the present analysis only the larger year classes (usually > 40 mm) were used to ensure complete recruitment. Under these two assumptions any variation around the linear relationship must represent variability in the set and survival of juveniles (Haukioja and Hakala, 1978). In a regression of $\text{Log}_e(N)$ on age the standard deviation of the residuals is then a measure of the

Table 1. Life-history parameters estimated for each population. Measurements of egg density and egg diameter represent late developing individuals. -: Missing value VJM: Variation in juvenile mortality DSI: Disease severity index

Sampling Site	Site Code	Date of Sampling	ω	VJM	Longevity (years)	Size of Maturation (mm)	Egg Density	Egg Diameter (μ m)	DSI	Proportion of Females (%) ^a
Tangler Sound MD	TS	27- 3-78	29.108	-.226	4.39	-	676	44.9	6.359	49.7 (167)
Big Annessex River MD	AR	27- 3-78	29.354	.301	4.84	-	495	36.6	2.801	57.8 (166)
Navesink River NJ	NR	2- 6-77	24.034	.212	15.03	27	-	-	2.155	48.9 (180)
Raritan Bay NJ	RB	1- 6-77	14.034	-.014	4.11	24	-	-	0.405	50.0 (194)
Winnapaug Pond RI	WP	18- 7-77	21.996	.050	13.13	20	-	-	6.545	55.3 (170)
Quonochontaug Pond-1 RI	Q1	22- 6-76	10.954	-.101	9.37	29	1515	38.9	-	56.7 (60)
Quonochontaug Pond-2 RI	Q2	4- 4-77	11.866	-.510	12.02	28	-	-	5.074	49.1 (159)
Saugatucket River RI	SR	14-12-78	15.329	-	14.07	32	-	-	-	54.2 (144)
Wickford RI	WK	15- 3-76	20.258	.273	8.34	-	1009	42.2	-	54.7 (190)
Coonamessett River MA	CR	12- 5-77	19.521	.220	14.15	-	-	-	6.581	51.1 (133)
Allen Harbor RI	AH	27- 9-77 ^b	10.222	-.352	12.25	19	1303	38.5	9.863	53.3 (283)
West Falmouth MA	WF	3- 5-77	12.538	-	9.67	21	-	-	6.914	52.7 (186)
New Bedford MA	NB	18-10-78	13.678	-.009	8.10	-	-	-	9.756	48.1 (156)
East Greenwich Cove RI	EG	3- 3-76 ^b	12.662	.051	7.10	17	890	38.4	-	51.6 (310)
Bourne MA	BN	22- 5-76	8.500 ^c	-	-	30	1285	40.4	-	50.3 (159)
Watchemoket Cove RI	WC	12- 5-76	12.301	.484	7.54	23	-	-	-	64.6 (82)
Portland ME	PT	21- 7-76	9.696	-.113	14.73	27	1318	25.9	-	54.3 (162)
Deer Isle ME	DI	22- 9-76 ^b	8.533	-.285	-	32	1541	35.9	4.512	50.3 (159)
Goose Cove ME	GC	20- 7-76	8.500 ^c	-	-	25	1414	35.1	-	52.2 (161)
Long Cove, Searsport ME	SP	22- 9-76 ^b	11.903 ^c	-	-	30	1260	35.1	10.289	52.7 (693)
Stockton Harbor ME	SH	13- 9-78	7.668	-.228	13.26	25	-	-	11.267	48.1 (156)
Perry ME	PY	15- 8-78	-	-	-	41	-	-	0.539	46.7 (167)
Robinston ME	RS	15- 8-78	11.869	.278	10.85	36	-	-	4.497	50.3 (185)
Janvrin Lagoon NS	JL	18- 7-78	5.103 ^c	-	-	27	-	-	4.976	51.9 (183)
Potato Island NS	PI	18- 7-78	8.041	-.031	9.79	28	1337	37.6	2.223	53.5 (198)

^a Total number of sexed individuals is given in parentheses

^b Supplementary samples were taken on other dates

^c Previously unreported estimate

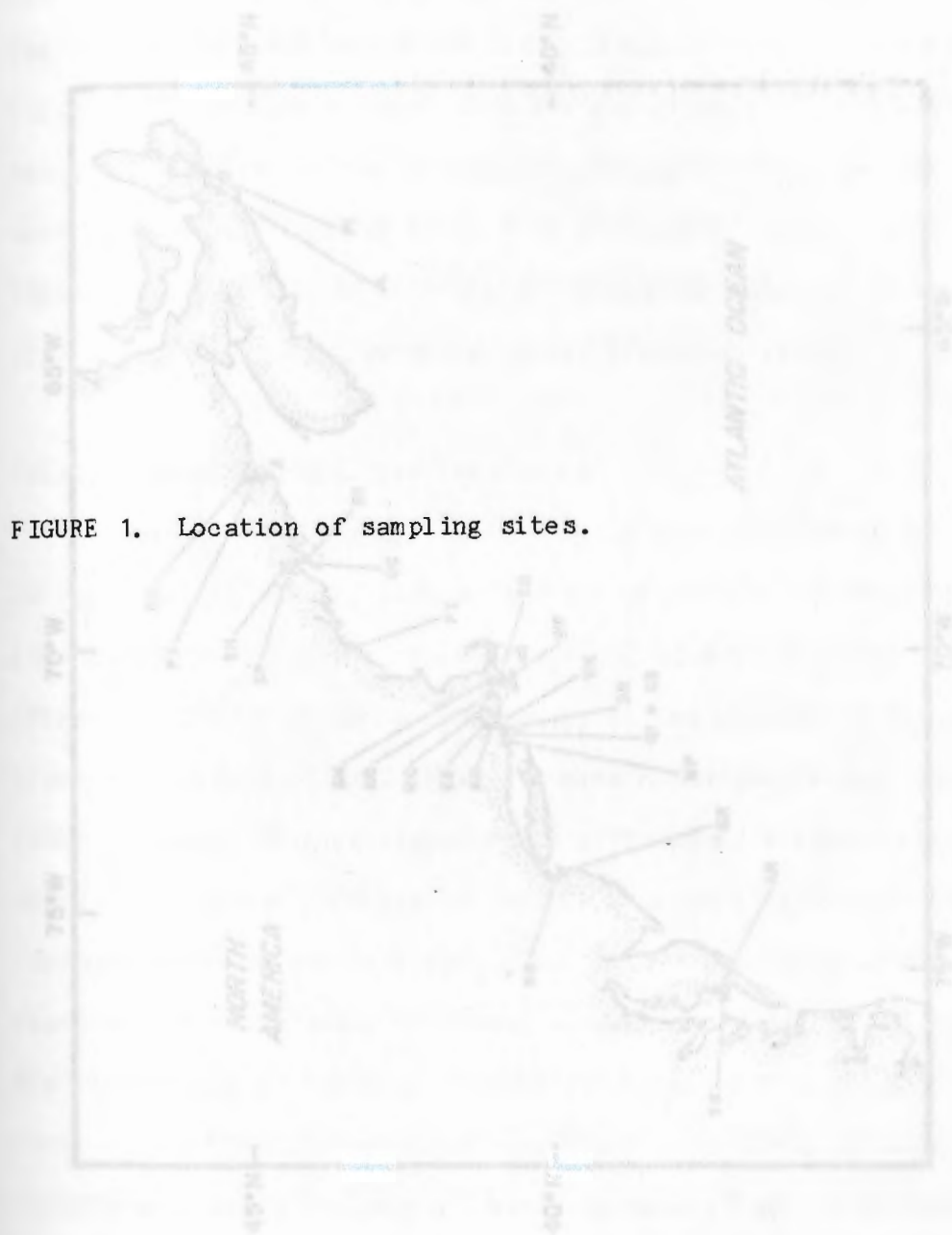
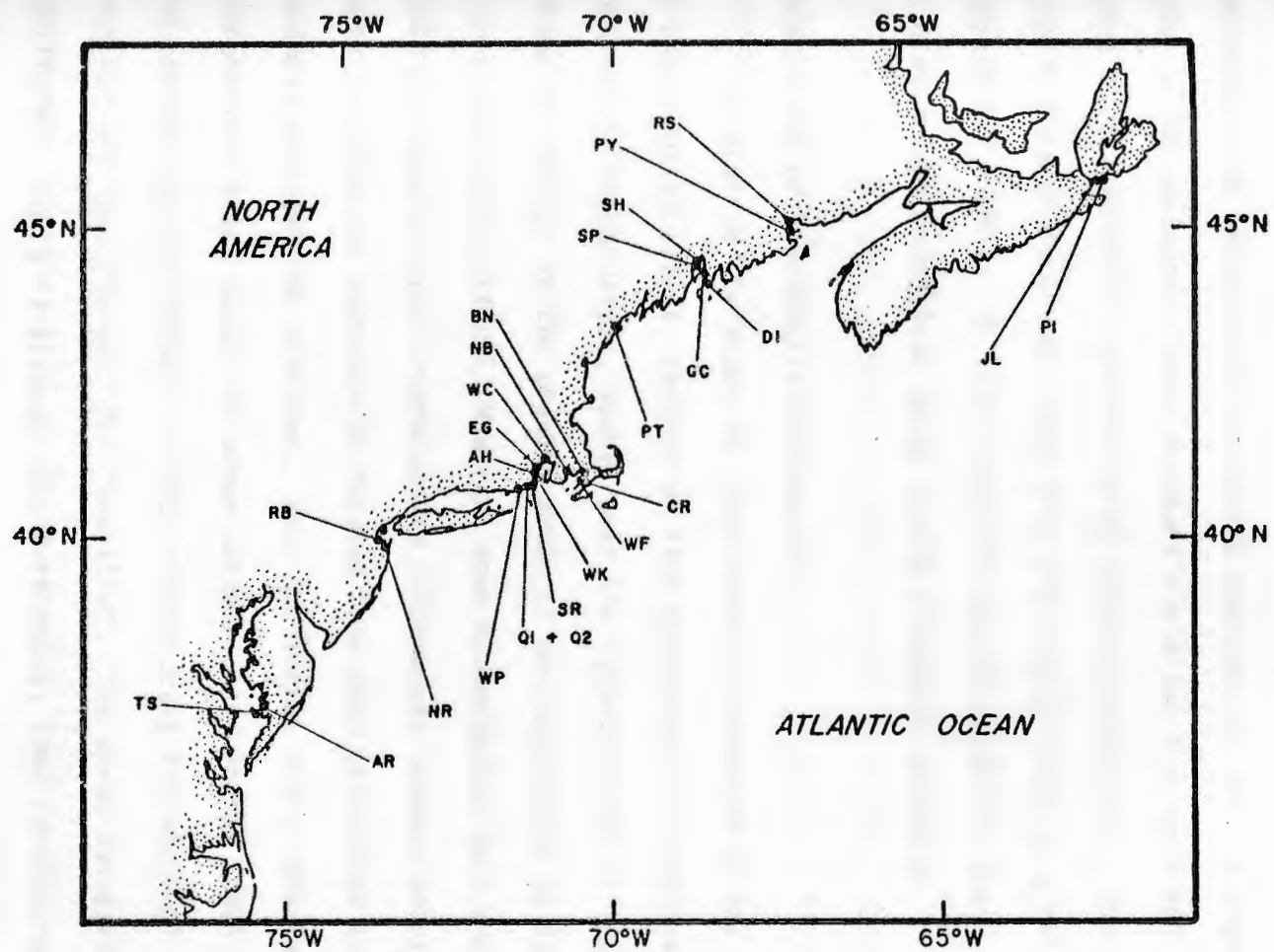


FIGURE 1. Location of sampling sites.



variation about the line. Since the standard deviation is somewhat dependent upon sample size a regression of the standard deviation against the number of age groups was made. The residuals from this regression are taken as the corrected estimate of VJM. A negative value would indicate a lower standard deviation than expected and hence a low degree of variability in juvenile mortality. The data used in this analysis was taken from a previous study on growth (Appeldoorn, 1980). In that study the age structure of each population was determined using length frequency analysis.

Calculation of Reproductive Parameters

Central to the study of life-history strategies is the concept of reproductive effort, defined as "the proportion of resources diverted to reproduction, summed over the time interval in question" (Stearns, 1976). In the present study it was impossible to estimate true reproductive effort. However, some measurements were made that could indicate relative reproductive differences between populations. Using histological sections 20 females from each population were randomly selected and examined. Each individual was classified as to reproductive stage using the seven categories of Porter (1974) and the terminology of Brousseau (1978b) substituting "developing" for "active" and "indifferent" for "inactive". The seven categories are: indifferent, early developing, mid-developing, late developing, ripe, partially spawned, and spent. As with previous studies (Ropes and Stickney, 1965; Porter, 1974; Brousseau, 1978b) the continuous nature of gametogenic activity often led to classification problems. Frequently clams at the spent stage contained new ova already

developing for a possible second spawn.

Egg diameters were measured on five ova per individual using an ocular micrometer. These data were converted to the average egg size at each observed reproductive stage.

Triplicate egg density counts were made for each individual. Egg density was defined as the number of eggs (with nucleus visible)/microscope field $\times .29 \text{ mm}^2$. Although based on a single section, these measurements were assumed to be reliable since Brousseau (1978b) found that egg densities remained constant throughout the gonad. These data were converted to the average egg density at each observed reproductive stage. The density estimates reflect the fecundity/unit of gonadal tissue, termed relative fecundity. Absolute fecundity could not be measured because variations in the relative gonadal volume could not be accounted for if indeed such variations took place.

Other Parameters

Sex proportions were calculated for each population by comparing the number of females to the total number of sexed individuals. All sex determinations were based on histological examination of the gonads.

Growth rate estimates were taken as the parameter ω (Gallucci and Quinn, 1979) of the von Bertalanffy growth model. These estimates were obtained from a previous detailed analysis of growth in these populations (Appeldoorn, 1980).

Longevity was crudely estimated by calculating the age of the largest individual collected at each site.

The size of sexual maturation was estimated as the size of the smallest female collected at each site. Size was measured instead of age because sexual maturation occurs when a clam reaches a certain size rather than a certain age (Belding, 1930; Coe and Turner, 1938; Hanks, 1963). In addition, the concept of increased cost of early maturation is easier to comprehend from the standpoint of size, especially given the wide variations in growth that occur between M. arenaria populations.

For some sites estimates for the pathological condition of the clam population were available. These were taken as the disease severity index (DSI) of Walker et al. (in press).

Calculation of Regressions

Geometric mean functional regressions were used in all cases due to the natural variability of both the x- and y-variables, and the small sample size (Ricker, 1973). In the regressions between population parameters no single parameter could be considered as the independent variable. As a standard, the growth parameter ω was somewhat arbitrarily chosen as the x-variate in these regressions. The rest of the parameters were then regressed against ω . All regressions were run using the GLM procedure of SAS79 (Helwig and Council, 1979). The predictive regression coefficient (slope) b was converted to the functional regression coefficient v through $v = b/r$ where r is the correlation coefficient. The significance of the regression can be tested by seeing if the 95% confidence interval around v ($= v \pm 2$ standard errors) brackets zero (Ricker, 1973).

RESULTS

Estimates of all the parameters used in the regressions are shown in Table 1.

Sex Proportions

From Table 1 it can be seen that in the majority of the populations females outnumbered males. The overall average proportion of females was 52.3%. The null hypothesis of equal sex ratios among all samples was tested using the Wilcoxon sign rank test (Hollander and Wolfe, 1973). The test showed that females significantly outnumbered males ($T^* = 2.874$, $p = .004$) so the null hypothesis was rejected.

VJM, Longevity, Maturation vs ω

Table 2 shows the results of the regression of VJM, longevity, and the size of maturation against growth. The regressions indicated that longevity was negatively related to growth while the size of maturation and variation in juvenile mortality were positively associated with growth. The size of maturation showed the weakest correlation. This might be expected since the realized size of maturation depends upon the present nutritional condition of the population (Coe and Turner, 1938). The genetically determined minimum size of maturation would be realized only if the nutritional requirements were met.

Egg Diameter and Egg Density vs ω

Table 2 also shows the results for the regressions of egg

Table 2. Results of the functional regressions. The slope of the predictive regression (b) can be found by $b=v \cdot r$

Regression	r	Intercept	v=slope	Approximate 95% Confidence Limits
VJM vs ω	.372	-0.575	0.038	0.020 < v < 0.055
Longevity vs ω	.278	18.473	-0.536	-0.785 < v < -0.287
Maturation Size vs ω	.190	36.557	-0.861	-1.361 < v < -0.360
Egg Size vs ω	.437	29.137	0.594	0.256 < v < 0.932
Egg Density vs ω	.903	1762.743	-42.320	-53.819 < v < -30.820

diameter and egg density against growth. These analyses were based solely on individuals classified as being in the late developing stage of reproduction. This stage was chosen because more populations had individuals in this stage than in any other. The data in Table 1 gives the average values for the late developing stage individuals. The regressions show a positive relationship between egg size and growth, and a strong negative relationship between egg density and growth.

Egg Diameter vs Egg Density

Table 3 illustrates the relationship between egg diameter and egg density in a series of pair-wise comparisons. The sample pairs consist of two sites sampled proximally in both time and space. Hence any apparent trends should represent differences due to variations in local conditions. The table shows evidence of a positive relationship between egg diameter and egg density. This relationship was tested using a binomial test (Hollander and Wolfe, 1973), and was found to be significant at $p=0.07$. At only 2 of the 7 sites for which comparisons of the pathological condition could be made did a poorer condition associate with a larger egg density and diameter. This relationship was similarly tested and found to become significant at $p=0.22$.

DISCUSSION

Sex Proportions

In previous studies on Mya arenaria Shaw (1965), Pfitzenmeyer (1972), Porter (1974), and Brousseau (1978b) all reported that the

Table 3. Pair-wise comparisons of egg density, egg diameter, and DSI. -: Missing value

Comparison	Larger Egg Density	Larger Egg Diameter	Smaller DSI
GC - PT	GC ^a	GC	-
JL - PI	JL ^b	JL	PI
PY - RS	RS ^c	PY	RS
EG - WK	WK ^a	WK	-
EG - BN	BN ^b	EG	-
EG - WC	WC ^b	EG	-
BN - WC	BN ^b	BN	-
AR - TS	TS ^a	TS	AR
AH - Q2	Q2 ^a	Q2	Q2
DI - SP	DI ^a	DI	DI
DI - SH	DI ^c	DI	DI
SP - SH	SP ^c	SP	SP

^a Comparisons involving reproduction were made using late developing individuals

^b Comparisons involving reproduction were made using ripe individuals

^c Comparisons involving reproduction were made using early developing individuals

porportion of females did not significantly differ from the proportion of males. Porter's study was the only one to give the actual figures. He found slightly more females (52%). The present finding of an unequal sex ratio is not unexpected, though. Unequal sex ratios are not uncommon in the mollusks, including the bivlaves and Fretter and Graham (1964) stated the females tend to out number males in gonochoristic species. Some examples of the percentage of females found in some bivalves are: Cardium (=Cerastoderma) edule 40%; Donax vittatus 45%; Tellina balthica 53%; T. fragilis 52%; Scrobicularia piperata 59%; Pholas candida 55%; and Anodonta cygnea 46% (Pelseneer, 1926). Normally in these species the disparity is not present in the young but increases with age. It is assumed to be due to a higher mortality rate for the males (Pelseneer, 1926). In the present study, populations with similar growth rates were pooled, and trends in the sex ratio were examined. No trend with size was apparent. The cause for this disparity remains enigmatic.

Life-History Strategy

Previous empirical and theoretical studies have identified two opposing life-history strategies: r- and K-selection, and bet-hedging (Stearns, 1976). Under conditions where environmental variability and density independent mortality affect the young more than the adults these two strategies yield contradictory predictions. In a fluctuating environment r- and K-selection predicts rapid development, early maturation, semelparity, large reproductive effort, more young, and shorter life; bet-hedging predicts just the opposite. Although contradictory results are predicted by the two

theories it is often difficult to classify a particular species because of complicating factors (Stearns, 1976).

In a previous study on growth and environmental variation it was found that there existed strong and fairly consistent environmental changes with latitude and that growth was correlated to this latitudinal trend (Appeldoorn, 1980). Growth decreased toward the north. In the following discussion some simplifications are made. It is assumed that a decrease in latitude represents an increase in growth and all results will be discussed in a north-south context. This is done strictly for convenience; to simplify the discussion of strategies exhibited by the observed trends in population parameters.

Mya arenaria produces vast numbers of planktotrophic larvae. Estimates of its fecundity range from 120,000/year by Brousseau (1978b) to 3 or 4 million/spawn¹ by Belding (1930) and 1 to 5 million/spawn by Stickney (1964). This high fecundity is consistent with the strategy of larval dispersal (Thorson, 1950). Concomitant with high fecundity is high mortality and as a species M. arenaria exhibits a basic pattern of high juvenile mortality and low adult mortality (Brousseau, 1978a). This juvenile mortality is by and large density independent (Ayers, 1956).

Overlying this basic pattern are two observable trends in

¹ For a 2.5 inch clam Belding reported a fecundity of 4 million in the text, but 3 million in a summary of Mya's life-history. Earlier publications of this work (Belding, 1907; 1916) gave no figures for absolute fecundity. It remains unclear which figure is correct although the latter figure is most often quoted (e.g. Turner, 1948; Ayers, 1956; Dow and Wallace, 1961; Brousseau, 1978b).

mortality. First, adult mortality increases toward the south. This is indicated by reduced longevity in the faster growing populations. Evidence for this trend is also found in the literature, with a reported life span for Mya of 5 years in Chesapeake Bay (Pfitzenmeyer, 1972), 12 years in Massachusetts (Belding, 1930), and over 20 years in Nova Scotia (Vandermeulen, 1977). This trend is probably due to temperature effects. Mya arenaria is a boreal species (Laurson, 1966) and is under temperature stress in the southern part of its range (Pfitzenmeyer, 1972). Second, juvenile mortality becomes more variable toward the south as evidenced by the positive correlation between w and VJM. This implies that the environment is more variable toward the south. In Chesapeake Bay Mya can be limited by high temperatures, low salinity, low dissolved oxygen (Pfitzenmeyer, 1972) and unsuitable substrate conditions (Pfitzenmeyer and Drobeck, 1963). Bayne (1965) showed with Mytilus edilis than any delay in finding a suitable substrate for settlement may exhaust energy reserves and prevent normal metamorphosis; a problem compounded by rapid metabolism at high temperatures. In addition, with increased submergence, southern populations are exposed to more consistent predation pressure after settlement.

These two opposing mortality trends would make any a priori prediction of a life-history strategy for Mya difficult. However, the trends observed in the present study reveal a consistent north-south pattern. (1) Growth rate increases. When the environment becomes more variable with respect to the juveniles the best strategy is to grow quickly and thereby escape the problems faced by small clams. With Mya, increased growth means an increase

in burial depth and protection from short-term adverse environmental conditions and predation. (2) On the basis of size there is a delay in maturation. Although not strong, this relationship is supported in the literature. The size of maturation is reported as 25 mm in Chesapeake Bay (Pfitzenmeyer, 1972), 20 mm in southern New England (Coe and Turner, 1938), and 15 mm in Maine (Hanks, 1963). Delayed reproduction allows more energy to be allocated toward early growth and also reduces the demand on resources already strained by high metabolic activity. Although a cost of reproduction has not been demonstrated for Mya, such a cost as measured by increased stress and mortality has been observed in Mytilus edulis (Bayne et al, 1978). The diverting of productivity toward growth in early life, however, results in an increased reproductive potential in later life due to a general fecundity-size relationship (Brousseau, 1978b). (3) Egg density decreases. Assuming equal gonadal volumes this would mean fewer eggs/brood. Since the possibility of a total reproductive failure from a single spawn increases towards the south, it would be advantageous to reduce the output/spawn but have more spawns. Ropes and Stickney (1965) gave evidence for such a trend in spawning. Northern populations spawned only once. Populations in the mid-range can spawn twice if conditions are favorable. The frequency of the second spawn increases towards the south. Two spawns are the rule in Chesapeake Bay (Pfitzenmeyer, 1962; 1965; Shaw, 1962; 1965). (4) Egg size increases. The production of larger eggs may be interpreted as an attempt to increase survival among the larvae. Studies by Vance (1973) and Crisp (1975) indicate that the planktotrophic larval strategy is optimized when the maximum number of eggs are produced

subject to the constraint that each egg contains the minimum energy reserve necessary for successful larval development to the feeding stage. Consistent with the increase in the VJM, a larger egg size would mean that towards the south Mya needs more energy for successful development. The work of Bayne et al. (1975; 1978) on Mytilus edulis and Helm et al. (1973) on Ostrea edulis has demonstrated that egg size has a very significant effect on the development and survival of larvae. Eggs with insufficient energy reserves result in smaller larvae, which remain planktonic longer, and have a decreased capacity for successful metamorphosis and survival.

To summarize: with decreasing latitude there is evidence for an association between an increase in the variability of juvenile mortality, faster growth, delayed maturation, reduced fecundity, more broods/year, and larger eggs. All these traits are consistent with the predictions of the bet-hedging strategy. The only anomalous and confounding trait is the increase in adult mortality already discussed. In variable environments bet-hedging predicts an increase in longevity coupled with a longer reproductive life. This clearly does not occur in Mya. However, the shortened reproductive life observed toward the south is somewhat offset by an increased frequency of spawning and a greater age-specific fecundity due to a larger age-specific size. A reduction in the total number of spawning seasons should be associated with a reduction in the juvenile mortality/adult mortality ratio (Stearns, 1976). In this sense the trends may be consistent since there is an increase in adult mortality toward the south while larger eggs may help reduce

juvenile mortality toward the south.

The above discussion considers the life-history adaptations of populations to environmental conditions. These are adaptations to long-term variations and are therefore assumed to be genetic in nature. Direct evidence of genetic differences in Mya arenaria is scarce. Morgan et al. (1975) did report genetic differences between clams from Chesapeake Bay and Maine. Clams from Chesapeake Bay were found to have greater polymorphism and heterozygosity.

Effects of Local Environmental Variability

Organisms adapt genetically to long-term environmental variations. Within that genetic framework there can also be physiological response to short-term variations in the environment. The evidence to date indicates that an increase in stress results in reduced reproduction. In the present study there was a correlation among proximal populations between egg density, egg size, and to a lesser degree pathological condition indicating that when conditions are good more and larger eggs are produced. Brouseau (1978b) found a direct relationship between egg size and fecundity when comparing spring and summer spawns and she showed that total fecundity could vary between both seasons and years. However, no connection was made between reproduction and the condition of the population. Coe and Turner (1938) reported that the number of young oocytes developing to mature ova was dependent upon the nutritional condition of the individual. These findings for Mya are consistent with those reported by Bayne (1972; 1976) and Bayne et al. (1975; 1978) for Mytilus edulis. They found that in stressed individuals fewer,

smaller eggs were produced resulting in larvae with reduced viability. It is assumed that under local conditions of stress Mya responds in a manner similar to that observed for Mytilus.

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