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

RICHARD S. APPELDOORN[1]

ABSTRACT

Age-length data and environmental parameters were obtained for 25 populations of the soft-shell clam, *Mya arenaria*. Growth rates were analyzed for 20 of the populations and variations in the growth rates 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 components analysis which 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. Temperature, tidal height, tidal position, and edaphic conditions systematically varied with latitude, with temperature being the dominant factor affecting growth. Growth was negatively correlated to both siltiness and sedimentary hydrocarbons.

The growth of the soft-shell clam, *Mya arenaria*, has been studied by many investigators (Wilton and Wilton 1929; Belding 1930; Newcombe 1936; Swan 1952; Brousseau 1979; and others), and much work has been done in assessing the importance of various environmental factors in 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). Because of local variations researchers often disagreed on the relative importance of each of these factors, and overall trends have not been firmly established.

The purpose of this study was to investigate various factors contributing to growth rate variations in soft clam populations and to demonstrate a methodology incorporating the analysis of multiple factors applicable to the above investigation. Of specific interest was the demonstration of a latitudinal trend in growth and the factors responsible for it, since such a relationship had yet to be quantified (Brousseau 1979). Principal components analysis was used to analyze multivariate environmental data, and the von Bertalanffy model was used for the analysis of growth, using the recently introduced growth rate parameter ω of Gallucci and Quinn (1979). This study represents one of the first applications of ω to investigate growth rate variations.

MATERIALS AND METHODS

Samples of *Mya arenaria* and environmental data were obtained from 25 sites located along the east coast of North America, from Maryland to Nova Scotia (Fig. 1). The sites were initially chosen and sampled as part of a study to investigate the relationship between environmental quality and neoplasia (Brown 1980), and as a result 1) the sites varied greatly in their environmental quality, 2) the sampling design employed was not specifically designed for the present study, and 3) it was therefore necessary to use proxy data in some cases to represent certain environmental characteristics. These drawbacks were not severely limiting, since the particular statistical techniques used could control much of the induced variability in the data. Estimates of the following environmental parameters were obtained: 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.

---

[1] Graduate School of Oceanography, University of Rhode Island, Kingston, R.I.; present address: Department of Marine Sciences, University of Puerto Rico, Mayagüez, Puerto Rico 00708.

Manuscript accepted June 1982.

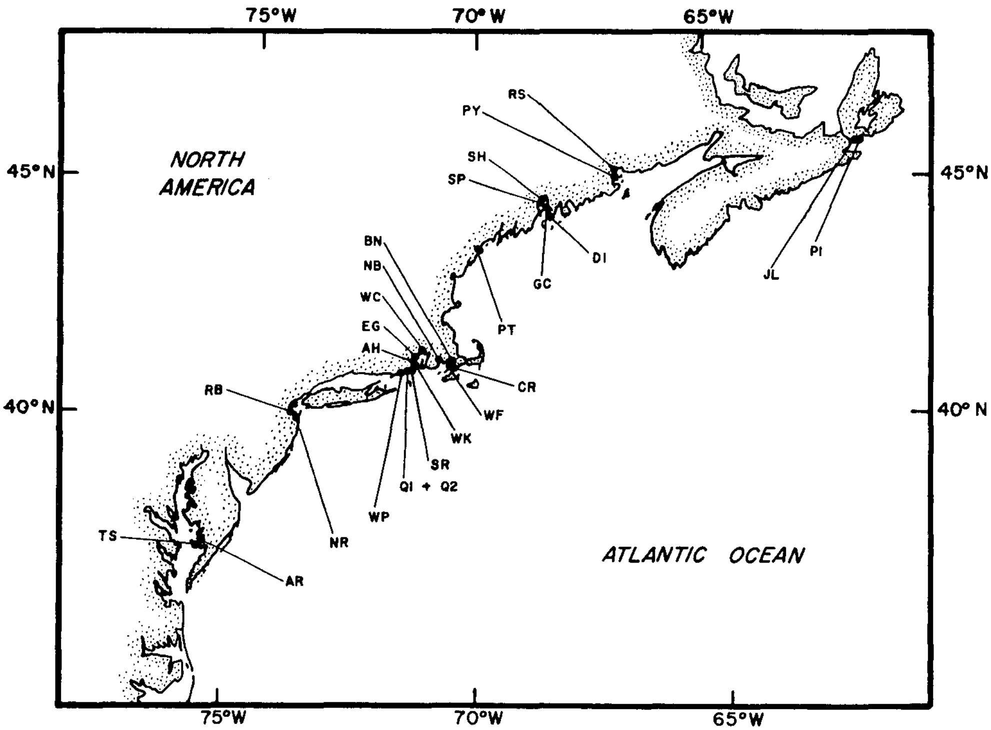

FIGURE 1.—Location of sampling sites. Site codes are given in Table 1.

Salinity, at low tide, was measured by a refractometer; tidal position was estimated on a scale of 0-1, where 0 = subtidal and 1 = full exposure. Estimates of the average annual temperature near each site were obtained from various literature sources, and estimates of the tidal range were obtained from National Ocean Survey (1978).

Sediment samples (composites of two surface cores 21 $\text{cm}^2 \times 8$ cm depth) were collected and analyzed to determine grain size distribution and organic content. The sand fraction was analyzed by dry sieving; silt-clay by the hydrometer method (American Society for Testing Materials 1963). The particle size distributions obtained from the two analyses 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 (Mdϕ), quartile deviation (QDϕ), and skewness (Skqϕ) (Buchanan 1971). The results were reported in phi notation rather than millimeters [$\phi = -\log_2(\text{mm})$], 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 percent organic matter was determined by measuring the percent weight loss of a small aliquot upon ignition at 550°C for 4 h (Buchanan 1971). Estimates for total sedimentary hydrocarbons through infrared analysis were obtained from C. Brown.[2] The sites and their environmental parameters are given in Table 1 along with their dates of collection, latitude, and code.

Clams were sampled from one or more trenches dug by a standard clam hoe or shovel, with the exception of the Chesapeake Bay sites where a commercial hydraulic escalator dredge was used. All clams excavated were retained for analysis. For each individual, shell length (maximum shell dimension) was measured by vernier calipers to the nearest millimeter.

Age structure was determined via length-frequency analysis for 19 of the populations. Similar information for six of the sites (BN, WF, SP, GC, PY, JL) was available from Appeldoorn (1981), though only the West Falmouth (WF) growth data were used in subsequent analyses since major growth interruptions resulting from pollution events occurred at the other sites.

---

[2] C. W. Brown, Professor, Department of Chemistry, University of Rhode Island, Kingston, R.I., pers. commun. May 1979.

TABLE 1.—Sampling sites and their environmental parameters. — = missing value.

Sampling site	Site code	Date of sampling	Latitude (°N)	Average annual temperature (°C)	Tidal range ft (m)	Tidal position	Mdϕ	QDϕ	Skqϕ	% silt-clay	% organic matter	Total sedimentary hydrocarbons (μg/g)	Salinity (ppt)
Tangier Sound, Md.	TS	27-3-78	37.952	[1]15.0	2.5 (0.77)	0	—	—	—	—	—	—	11
Big Annemessex River, Md.	AR	27-3-78	38.051	[1]15.0	2.5 (0.77)	0	—	—	—	—	—	—	11
Navesink River, N.J.	NR	2-6-77	40.377	[2]13.0	3.5 (1.08)	0.50	1.80	0.40	−0.10	1.0	1.5	114	24
Raritan Bay, N.J.	RB	1-6-77	40.459	[2]13.0	6.0 (1.85)	0.50	2.55	0.44	−0.05	4.2	2.6	104	24
Winnapaug Pond, R.I.	WP	18-7-77	41.327	[3]12.3	2.0 (0.62)	0.50	1.97	0.62	0.01	1.5	0.7	21	31
Quonochontaug Pond-1, R.I.	Q1	22-6-76	41,333	[3]12.3	2.0 (0.62)	0.35	1.00	0.60	0.00	0.7	1.5	0	31
Quonochontaug Pond-2, R.I.	Q2	4-4-77	41.333	[3]12.3	2.0 (0.62)	0.50	3.05	0.31	−0.01	8.1	1.5	9	31
Saugatucket River, R.I.	SR	14-12-78	41.423	[3]12.3	3.0 (0.92)	0.35	1.40	1.48	−0.40	2.0	1.1	509	16
Wickford, R.I.	WK	15-3-76	41.566	[4]10.5	4.7 (1.45)	0.35	2.92	0.23	−0.02	4.6	1.4	[5]15	27
Coonamessett River, Mass.	CR	12-5-77	41.577	[6]11.0	4.0 (1.23)	0	1.10	0.59	−0.05	2.7	1.0	101	12
Allen Harbor, R.I.	AH	27-9-77	41.620	[4]12.4	4.5 (1.38)	0.50	4.20	0.48	−0.03	61.1	1.9	358	28
West Falmouth, Mass.	WF	3-5-77	41.633	[6]10.5	5.0 (1.54)	0.50	0.46	0.80	0.27	2.1	0.8	190	32
New Bedford, Mass.	NB	18-10-78	41.639	[6]10.5	4.0 (1.23)	0.35	1.39	0.72	0.07	3.0	1.5	567	22
East Greenwich Cove, R.I.	EG	3-3-76	41.656	[4]11.5	5.0 (1.54)	0.20	2.08	1.08	−0.66	3.6	1.6	[7]24	19
Bourne, Mass.	BN	22-5-76	41.682	[6]10.5	3.8 (1.17)	0.50	0.89	0.55	0.01	2.4	0.7	523	30
Watchemoket Cove, R.I.	WC	12-5-76	41.799	[4]11.1	5.7 (1.75)	0.50	—	—	—	—	—	—	25
Portland, Me.	PT	21-7-76	43.636	[8]9.1	10.4 (3.20)	0.50	1.56	1.14	0.11	16.2	2.5	209	27
Deer Isle, Me.	DI	22-9-76	44.203	[9]7.4	11.2 (3.45)	0.80	1.90	1.38	0.57	9.8	1.6	24	32
Goose Cove, Me.	GC	20-7-76	44.377	[10]7.1	11.1 (3.42)	0.80	−0.51	1.37	0.09	2.8	1.4	254	20
Long Cove, Searsport, Me.	SP	22-9-76	44.463	[10]7.1	11.5 (3.51)	0.65	1.52	1.67	0.90	15.9	2.9	135	25
Stockton Harbor, Me.	SH	13-9-78	44.464	[10]7.1	11.5 (3.51)	0.65	0.26	2.05	0.15	7.3	1.3	399	25
Perry, Me.	PY	15-8-78	44.973	[9]6.7	21.0 (6.46)	0.65	2.22	1.58	−1.38	5.2	2.4	23	30
Robinston, Me.	RS	15-8-78	45.106	[9]6.8	21.0 (6.46)	0.65	−0.41	1.53	0.27	9.6	2.2	44	28
Janvrin Lagoon, Nova Scotia	JL	18-7-78	45.458	[11]9.0	4.0 (1.23)	0.65	2.24	0.46	0.06	8.2	1.4	177	29
Potato Island, Nova Scotia	PI	18-7-78	45.589	[11]9.0	4.0 (1.23)	0.65	−0.67	1.58	0.15	10.3	4.6	20	29

[1] Beaven (1960).
[2] Jeffries (1962).
[3] Marine Research (1975).
[4] Hicks (1963).
[5] Estimated from clam tissue concentration.
[6] Gilbert (1973).
[7] Estimated from gas chromatography measurement.
[8] Gilfillan et al. (1976).
[9] Welch (1981) and R. L. Dow, Maine Department of Marine Resources, State House, Augusta, ME 04333, pers. commun. January 1976.
[10] Shorey (1973).
[11] Sameoto (1972) and Thomas (1978).

Length-frequency analysis was chosen because it could be applied to all samples, thus facilitating the comparison between samples. The use of shell annuli is unreliable south of Cape Cod (Mead and Barnes 1904; Shuster 1951), and MacDonald and Thomas (1980) found little support for the technique in a Prince Edward Island population. Constraints on the sampling design precluded mark-recapture methods.

For each population the modes on a length-frequency histogram were broken down into a series of normal curves (Tesch 1971; MacDonald and Pitcher 1979) by a Dupont[3] 310 Curve Resolver, an analog computer which allows one to break down a complex distribution into its basic components in a graphical fashion (Appeldoorn 1981). From the resulting graphs the mean and standard deviation of the curve which represents each mode of the histogram can be obtained. The curve resolver also determines the percentage of the whole sample under each curve.

Length-frequency analysis assumes that spawning and settlement are discrete relative to growth such that the length distributions of cohorts are separable. Ropes and Stickney (1965), Pfitzenmeyer (1962), and Brousseau (1978) found that periods of both spawning and settlement of each cohort were discrete events. In the latter study, closely spaced cohorts within the same year were separable by length-frequency analysis using probability paper. In the present study, discrimination of cohorts within a year class was also possible.

By inspection of the histograms and subsequent age-length curves and through consideration of local recruitment processes and sampling efficiency, ages were assigned to each cohort (Brothers 1980; Schnute and Fournier 1980). When possible, results were corroborated by comparing them with previously published age-length data for the same or nearby areas (e.g., Belding 1930; Pfitzenmeyer 1972; Mead and Barnes 1904; Gilfillan and Vandermuelen 1978; Brousseau 1979), by comparison of adjacent areas (e.g., the two Quonochontaug Pond sites), by comparison of multiple samplings (Allen Harbor, Deer Isle), and by counts of shell annuli (Portland, Deer Isle).

The ages assigned were relative rather than absolute; the time beyond the last yearly increment represents the fraction of expected yearly growth already obtained (Appeldoorn 1981). This process results in a smoother growth curve, since it linearizes seasonal growth variations which would otherwise necessitate the use of a more complex growth model (Cloern and Nichols 1978).

The analysis of growth differences can be simplified by comparing model parameters rather than the direct age-length observations (Rao 1958). Growth was modeled by fitting the von Bertalanffy growth function (VBGF) to the age-length data. The VBGF is described by the equation:

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

where t = time, L_t = length at time t, L_∞ = maximum asymptotic length, K = growth constant, and t_0 = time when $L_t = 0$. The single growth parameter of Gallucci and Quinn (1979) is obtained by $\omega = K \cdot L_\infty$.

Recent studies on the statistical comparison of VBGF's (Allen 1976; Bayley 1977; Gallucci and Quinn 1979; Kimura 1980; Misra 1980; Kappenman 1981) and on the VBGF's biological basis (Pauly 1979, 1981) have removed most of its past criticism (Roff 1980). Dickie (1971) considered the VBGF applicable for modeling population growth even when individual growth did not fit the model. The VBGF has been previously applied to *Mya arenaria* by Munch-Petersen (1973), Brousseau (1979), and Brêthes and Desrosiers (1981).

The ω parameter was chosen for analysis because, as a single parameter, it was easily calculated, tractable to further analysis, statistically comparable, interpretable in both a biological and statistical sense, and more robust than either K or L_∞ (Gallucci and Quinn 1979). A major benefit of applying the VBGF is that only estimates of length at known time intervals are required to determine K, L_∞, and hence ω. 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, but only a location parameter.

The VBGF was fitted to the data according to the methods of Gallucci and Quinn (1979), using the NLIN procedure of SAS79 (Helwig and Council 1979) which yielded estimates of the parameters, their asymptotic standard errors, and the correlation coefficient of K and L_∞. From these estimates the ω parameter and its variance were calculated (Gallucci and Quinn 1979). The regression procedure incorporated the size and

---

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

variance of each age mode. Therefore, variation in the original data is reflected in the variance estimates of the model parameters, and poorly represented age modes, where estimates of mean length and variance might be subject to error, are weighted less. The resulting growth curves are based on the assumption that growth varies from year to year only to the extent expected owing to normal fluctuations in growing conditions. Hence, they are an estimation of "average" growth within a population, representing an integration of several variable processes affecting growth.

The environmental data listed in Table 1 were used to characterize *Mya arenaria* habitats. These data were subjected to principal components analysis (PCA) to reduce the observed variables to a more meaningful and manageable number of factors without excessive loss of information. PCA locates hidden components which have generated dependence in the observed variables (Morrison 1976). Each resulting component is a composite variable—a linear combination of the original variables. The components are independent and ordered, so that the first component accounts for most of the observed variation, the second for most of the residual variation, and so on. The loadings given for each component represent the correlation coefficient (r) between a variable and 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 measure) by using the CORR, FACTOR, and SCORE procedures of SAS79 (Helwig and Council 1979).

The components produced by PCA are limited by the input data and can only reflect the factors represented by those data. In the present study the selection of factors was constrained by the sampling design, and no direct measurements were made on a number of factors which would be expected to influence growth (e.g., current flow, food concentration). However, several of the factors represent an integration of processes, incorporating factors not measured directly. For example, current flow is represented to some degree by tidal range, tidal position, and sediment characteristics (see Discussion). This integration effect will help offset the limitations of the input data.

The growth rate parameter was transformed to $\log_{10}(\omega)$ for the analysis of growth variations. Since $\log_{10}(K)$ and $\log_{10}(L_\infty)$ are inversely proportional (Pauly 1979), it is felt that $\log_{10}(\omega)$ is a more suitable measure of growth (Appeldoorn in press). A difference in $\log_{10}(\omega)$ would then indicate a fundamental difference in growth—not just a reciprocal change in K and L_∞. [See Pauly 1979, 1980 for a discussion of the analogous $P = \log_{10}(K \cdot W_\infty)$ parameter of the VBGF for weight.]

Variations in growth rate were analyzed using a stepwise functional regression of $\log_{10}(\omega)$ on the components generated by PCA, where the residuals of the regression of the $\log_{10}(\omega)$ on Component 1 were regressed against Component 2 and so on. The geometric mean functional regression was deemed appropriate because of variability in both ω and the components, small sample size, and uncertainties about the distribution of the data (Ricker 1973; Laws and Archie 1981). In normal predictive regressions the regression coefficient (slope) is b; functional regression yields a coefficient of $v = b/r$ where r is the correlation coefficient. The standard error of v (SE_v) equals the standard error of b (SE_b) and 95% confidence limits on v are approximated by $v \pm 2SE_v$ (Ricker 1973). Estimates of b, r^2, and SE_b were obtained using the GLM procedure of SAS79 (Helwig and Council 1979) and used to calculate v and its 95% confidence limits. The significance of the regression is tested by determining if the confidence limits bracket $v = 0$. If not, the null hypothesis H_0: $v = 0$ is rejected.

RESULTS

The mean lengths at age as determined through length-frequency analysis are given in Appendix Table 1 for the 19 populations analyzed here. The parameters of the VBGF and $\log_{10}(\omega)$ are given in Table 2. Using the 95% confidence limits around $\log_{10}(\omega)$, statistically significant growth differences become readily apparent. A functional regression of $\log_{10}(\omega)$ on latitude yielded: $\log_{10}(\omega) = 4.8184 - 0.0878$ latitude with $r = 0.8220$. Although the regression accounts for the majority of the observed variation in growth, it does not indicate what underlying processes may be responsible for this relationship.

The results of the PCA are shown in Table 3. The terms used in the table follow the definitions in Morrison (1976). In order to simplify the table, those loadings <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 greater detail.

TABLE 2.—Estimates and standard errors for the von Bertalanffy constants.

Site code	K	L_∞	t_0	$\text{Log}_{10}(\omega)$ +	95% confidence interval
TS	0.2530 (0.0597)	111.05 (11.18)	−1.188 (0.263)	1.4486	1.3839-1.5050
AR	0.2740 (0.0520)	107.13 (7.22)	−1.440 (0.268)	1.4677	1.4166-1.5134
NR	0.3016 (0.0162)	79.69 (1.10)	−0.718 (0.095)	1.3808	1.3473-1.4119
RB	0.1829 (0.0986)	81.50 (22.08)	−1.450 (0.558)	1.1734	1.1202-1.2207
WP	0.2992 (0.0114)	73.27 (0.89)	−0.400 (0.058)	1.3418	1.3253-1.3577
Q1	0.1175 (0.0194)	93.23 (9.20)	−1.104 (0.148)	1.0396	0.9848-1.0882
Q2	0.1069 (0.0134)	111.00 (6.96)	−1.205 (0.191)	1.0743	1.0045-1.1344
SR	0.2119 (0.0229)	72.34 (2.48)	−0.445 (0.225)	1.1855	1.1417-1.2253
WK	0.1811 (0.0155)	111.80 (4.21)	−0.436 (0.127)	1.3066	1.2724-1.3383
CR	0.1997 (0.0114)	97.75 (1.60)	−0.990 (0.143)	1.2905	1.2512-1.3265
AH	0.0903 (0.0184)	113.20 (13.11)	−1.668 (0.288)	1.0095	0.9147-1.0873
WF	0.0917 (0.0162)	136.73 (14.88)	−1.357 (0.184)	1.0982	1.0056-1.1746
NB	0.1532 (0.0198)	89.28 (4.30)	−1.571 (0.304)	1.1360	1.0902-1.1774
EG	0.1377 (0.0425)	91.95 (18.20)	−0.914 (0.186)	1.1025	1.0439-1.1541
WC	0.1411 (0.0246)	87.18 (7.37)	−1.549 (0.236)	1.0899	0.9965-1.1668
PT	0.1468 (0.0077)	67.91 (1.39)	−0.836 (0.122)	0.9986	0.9778-1.0186
DI	0.1255 (0.0114)	67.96 (2.46)	−0.781 (0.218)	0.9311	0.8974-0.9623
SH	0.0565 (0.0083)	135.71 (12.34)	−0.980 (0.336)	0.8847	0.7663-0.9776
RS	0.1623 (0.0287)	73.13 (4.52)	−0.745 (0.434)	1.0754	1.0275-1.1167
PI	0.0986 (0.0248)	81.55 (10.78)	−0.171 (0.432)	0.9053	0.7839-0.9674

TABLE 3.—Results of the principal components analysis on environmental data. Loadings <0.30 have been omitted for clarity.

Environmental parameter	Principal components					Communality
	1	2	3	4	5	
Average temperature	−0.938					0.925
Tidal range	0.806			0.383		0.819
Tidal position	0.817					0.855
Mdϕ	−0.503	0.725				0.891
QDϕ	0.808	−0.382				0.872
Skqϕ			0.386	−0.858		0.933
% silt-clay		0.609	0.675			0.880
% organic matter	0.521				0.765	0.942
Total hydrocarbons			0.802			0.855
Salinity	0.396	0.750				0.840
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	88.0	

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. It decreases with latitude. To avoid confusion the first component will be referred to as "northness." The second component is sediment siltiness. 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; Knauss 1978). The third component, positively correlated with hydrocarbons and percent silt-clay, is sedimentary hydrocarbons. The higher silt-clay component (also reflected to some degree by positive skewness) provides a greater sedimentary surface area for the retention of hydrocarbons (Lytle and Lytle 1977).

The first three components were used for the further analysis of growth to try and deduce factors which could have contributed to the latitudinal trend and to point out secondary growth affecting factors. Several sites were omitted from this analysis because missing values precluded the calculation of the component scores. The results of the stepwise regression analysis are given in Table 4. As expected, growth was found to be negatively correlated with northness. The second regression showed a negative relationship between siltiness and growth. The last

TABLE 4.—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	0.693	1.1137	−0.1653	$-0.2269 < v < -0.1037$
1st residual vs. siltiness	0.184	−0.0112	−0.1116	$-0.1682 < v < -0.0549$
2d residual vs. sedimentary hydrocarbons	0.217	0.0065	−0.1472	$-0.2214 < v < -0.0730$

regression indicated that growth was negatively correlated with sedimentary hydrocarbons.

DISCUSSION

The observed relationship between latitude and growth rate is not surprising, especially considering the range of temperatures reflected in the data. Increasing growth would be expected at higher temperatures owing to temperature's direct effect on metabolism and length of the growing season (Brousseau 1979). In addition, with increasing temperature *Mya* is found lower intertidally or even subtidally (Pfitzenmeyer 1972), 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 quantify such a latitudinal relationship. Newcombe (1936) and Turner (1948) each noticed growth differences between three populations which they attributed to temperature. Brousseau (1979) showed a tendency for Massachusetts populations to grow faster than more northern ones, but the relationship was not definite. Each of these studies suffered from two deficiencies: Limited geographical range and small number of sample sites. Under these limitations, variations in growth rate due to local conditions can mask any latitudinal trends. The unaccounted variation (32%) in the regression of $\log_{10}(\omega)$ on latitude is evidence for this.

Analysis of the latitudinal trend of growth rate and its residual variation was facilitated by the PCA results. The first component, northness, correlated well with growth. Temperature and tidal position had the highest loadings for this component; their interrelationship and influence on growth have already been discussed. As with many factors, the components produced by PCA represent an integration of effects and the correlation between growth and northness may depend upon factors other than temperature.

Two other characteristics vary markedly with increasing northness. The sediment becomes coarser and more variable, and tidal range increases. The tidal range increase, due to the large tides of the Gulf of Maine and Bay of Fundy, represents to some degree an increase in tidal current. Belding (1930) considered current the most important factor affecting growth. Coarser sediments are beneficial to growth by allowing for ample water percolation, drainage, and exchange (Dow and Wallace 1961; Swan 1952). The correlation of northness with coarser, variable sediments reflects both their glacial origins and the influence of current on their deposition.

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 effect of siltiness on growth also represents an integration of processes. In small quantities silt and clay help stabilize surface sediments (Kellogg 1905), but in large quantities they become detrimental. Studies with *Mya arenaria* have shown that excessive siltation can lead to reduced feeding through clogging of the gills (Belding 1930), to growth interruptions when silt becomes trapped between the shell and mantle (Shuster 1951), and to complete smothering and death (Wilton and Wilton 1929; Dow and Wallace 1961). Silty sediments tend to be fairly consolidated, and reduced growth has been observed in such sediments (Swan 1952; Dow and Wallace 1961). High silt-clay is also indicative 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 PCA, were 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 1981). Hydrocarbon pollution can adversely affect growth through direct toxicity, smothering, and sediment compaction.

CONCLUSIONS ON METHODOLOGY

PCA produced meaningful, easily interpretable variables which led to results, when further analyzed, that were lucid, rational, and consistent with other studies. Since PCA will be limited by the input data, sampling should be properly designed or controlled. One advantage of PCA is that variable integration effects can incorporate some factors not specifically measured. However, reliance upon these effects should be avoided when possible and caution should be exercised when interpreting the results.

The ω parameter proved useful, both for its description of growth rate and ease of manipulation in further analyses. Incorporating both the sample size and variance of the age-length determinations into the nonlinear regression protected ω against random errors in the location of the age-length modes. In addition, since ω is more robust than either K or L_∞, it is further protected against inaccuracies in their estimation—an advantage over using K during the subsequent growth analyses. The trends resulting from the subsequent regressions were also protected from random inaccuracies in the estimation of ω by virtue of the large number of sample sites used. However, it is important to recognize that such random errors do exist and not to continue the analysis past its potential limits.

ACKNOWLEDGMENTS

The author wishes to express his gratitude to those people who assisted in the clam collection, particularly R. L. Dow, M. Richards, J. M. Hickey, M. L. H. Thomas, and M. Worobec; and to those people who were involved in the sample processing, notably R. S. Brown, J. Keller, A. Miller, S. Polofsky, C. Brown, and E. Franklin. S. B. Saila, A. N. Sastry, R. C. Bullock, and two journal reviewers gave helpful criticism. Financial support for sample collection was provided by the American Petroleum Institute.

LITERATURE CITED

ALLEN, R. L.
1976. Method for comparing fish growth curves. N.Z. J. Mar. Freshwater Res. 10:687-692.

AMERICAN SOCIETY FOR TESTING MATERIALS.
1963. Grain-size analysis of soils. D422-63. A.S.T.M. Standards 11:205-216.

APPELDOORN, R. S.
1981. Response of soft-shell clam (*Mya arenaria*) growth to onset and abatement of pollution. J. Shellfish Res. 1: 41-49.
In press. Relationships between the parameters of the von Bertalanffy growth function among bivalves as revealed with the auximetric grid. [Abstr.] J. Shellfish Res.

BAYLEY, P. B.
1977. A method for finding the limits of application of the von Bertalanffy growth model and statistical estimates of the parameters. J. Fish. Res. Board Can. 34:1079-1084.

BEAVEN, G. F.
1960. Temperature and salinity of surface water at Solomons, Maryland. Chesapeake Sci. 1:2-11.

BELDING, D. L.
1930. The soft-shelled clam fishery of Massachusetts. Mass. Dep. Conserv., Div. Fish. Game, Mar. Fish. Sect., Mar. Fish. Ser. 1, 65 p.

BRÊTHES, J.-C. F., AND G. DESROSIERS.
1981. Estimation of potential catches of an unexploited stock of soft-shell clam (*Mya arenaria*) from length composition data. Can. J. Fish. Aquat. Sci. 38:371-374.

BROTHERS, D. T.
1980. Age and growth studies on tropical fishes. *In* S. B. Saila and P. M. Roedel (editors), Stock assessment for tropical small scale fisheries, p. 119-136. Int. Cent. Mar. Resour. Dev., Kingston, R.I.

BROUSSEAU, D. J.
1978. Spawning cycle, fecundity, and recruitment in a population of soft-shell clam, *Mya arenaria*, from Cape Ann, Massachusetts. Fish. Bull., U.S. 76:155-166.
1979. Analysis of growth rate in *Mya arenaria* using the von Bertalanffy equation. Mar. Biol. (Berl.) 51:221-227.

BROWN, R. S.
1980. The value of the multidisciplinary approach to research on marine pollution effects as evidenced in a three-year study to determine the etiology and pathogenesis of neoplasia in the soft-shell clam, *Mya arenaria*. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 179:125-128.

BUCHANAN, J. B.
1971. Sediments. *In* N. A. Holme and A. D. McIntyre (editors), Methods for the study of marine benthos, p. 30-52. Blackwell Sci. Publ., Oxford.

CLOERN, J. E., AND F. H. NICHOLS.
1978. A von Bertalanffy growth model with a seasonally varying coefficient. J. Fish. Res. Board Can. 35:1479-1482.

DICKIE, L. M.
1971. Addendum: Mathematical models of growth. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 126-130. Blackwell Sci. Publ., Oxford.

DOW, R. L.
1975. Reduced growth and survival of clams transplanted to an oil spill site. Mar. Pollut. Bull. 6:124-125.

DOW, R. L., AND J. W. HURST, JR.
1975. The ecological, chemical and histopathological evaluation of an oil spill site. Part I. Ecological studies. Mar. Pollut. Bull. 6:164-166.

DOW, R. L., AND D. E. WALLACE.
1961. The soft-shell clam industry of Maine. U.S. Fish Wildl. Serv., Circ. 110, 36 p.

GALLUCCI, V. F., AND T. J. QUINN II.
1979. Reparameterizing, fitting, and testing a simple growth model. Trans. Am. Fish. Soc. 108:14-25.

GILBERT, M. A.
1973. Growth rate, longevity and maximum size of *Macoma balthica* (L.). Biol. Bull. (Woods Hole) 145:119-126.

GILFILLAN, E. S., D. MAYO, S. HANSON, D. DONOVAN, AND L. C. JIANG.
1976. Reduction in carbon flux in *Mya arenaria* caused by a spill of No. 6 fuel oil. Mar. Biol. (Berl.) 37:115-123.

GILFILLAN, E. S., AND J. H. VANDERMEULEN.
1978. Alterations in growth and physiology of soft-shell clams, *Mya arenaria*, chronically oiled with Bunker C

from Chedabucto Bay, Nova Scotia, 1970-76. J. Fish. Res. Board Can. 35:630-636.

HELWIG, J. T., AND K. A. COUNCIL.
1979. SAS user's guide, 1979 ed. SAS Inst. Inc., Raleigh, N.C., 494 p.

HICKS, S. D.
1963. Physical oceanographic studies of Narragansett Bay, 1957 and 1958. U.S. Fish Wildl. Serv., Spec. Sci. Rep.—Fish. 457, 30 p.

JEFFRIES, H. P.
1962. Environmental characteristics of Raritan Bay, a polluted estuary. Limnol. Oceanogr. 7:21-31.

KAPPENMAN, R. F.
1981. A method for growth curve comparisons. Fish. Bull., U.S. 79:95-101.

KELLOGG, J. L.
1905. Conditions governing existence and growth of the soft clam (*Mya arenaria*). Rep. Comm. year ending June 30, 1903, 29:195-224.

KIMURA, D. K.
1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull., U.S. 77:765-776.

KNAUSS, J. A.
1978. Introduction to physical oceanography. Prentice-Hall, Inc., Englewood Cliffs, N.J., 338 p.

KRUMBEIN, W. C., AND L. L. SLOSS.
1963. Stratigraphy and sedimentation. W. H. Freeman, San Franc., 660 p.

LAWS, E. A., AND J. W. ARCHIE.
1981. Appropriate use of regression analysis in marine biology. Mar. Biol. (Berl.) 65:13-16.

LYTLE, J. S., AND T. F. LYTLE.
1977. Sediment hydrocarbons as environmental indicators in the northeast Gulf of Mexico. *In* D. A. Wolfe (editor), Fate and effects of petroleum hydrocarbons in marine ecosystems and organisms, p. 404-412. Pergamon Press, N.Y.

MACDONALD, B. A., AND M. L. H. THOMAS.
1980. Age determination of the soft-shell clam *Mya arenaria* using shell internal growth lines. Mar. Biol. (Berl.) 58:105-109.

MACDONALD, P. D. M., AND T. J. PITCHER.
1979. Age-groups from size-frequency data: A versatile and efficient method of analyzing distribution mixtures. J. Fish. Res. Board Can. 36:987-1001.

MARINE RESEARCH.
1975. Charleston study annual report. April 1974 - March 1975. Mar. Res. Inc., Falmouth, Mass., 241 p.

MEAD, A. D., AND E. W. BARNES.
1904. Observations on the soft-shell clam (fifth paper). R.I. Comm. Inland Fish., 34th Annu. Rep., p. 29-68.

MISRA, R. K.
1980. Statistical comparisons of several growth curves of the von Bertalanffy type. Can. J. Fish. Aquat. Sci. 37:920-926.

MORRISON, D. F.
1976. Multivariate statistical methods. 2d ed. McGraw-Hill, Inc., N.Y., 415 p.

MUNCH-PETERSEN, S.
1973. An investigation of a population of the soft clam (*Mya arenaria* L.) in a Danish estuary. Medd. Dan. Fisk. Havunders., New Ser. 7:47-73.

NATIONAL OCEAN SURVEY.
1978. Tide tables 1979: High and low water predictions. East coast of North and South America, including Greenland. Natl. Oceanic Atmos. Admin., Natl. Ocean Surv., Rockville, Md., 293 p.

NEWCOMBE, C. L.
1936. A comparative study of the abundance and the rate of growth of *Mya arenaria* L. in the Gulf of St. Lawrence and Bay of Fundy regions. Ecology 17:418-428.

NEWCOMBE, C. L., AND H. KESSLER.
1936. Variations in growth indices of *Mya arenaria* L. on the Atlantic coast of North America. Ecology 17: 429-443.

PAULY, D.
1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. Berichte aus dem Institut fur Meereskunde 63, 156 p.
1980. A new methodology for rapidly acquiring basic information on tropical fish stocks: growth, mortality, and stock recruitment relationships. *In* S. B. Saila and P. M. Roedel (editors), Stock assessment for tropical small scale fisheries, p. 154-172. Int. Cent. Mar. Resour. Dev., Kingston, R.I.
1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Meeresforschung 28:251-282.

PFITZENMEYER, H. T.
1962. Periods of spawning and setting of the soft-shell clam, *Mya arenaria*, at Solomons, Maryland. Chesapeake Sci. 3:114-120.
1972. Tentative outline for inventory of molluscs: *Mya arenaria* (soft-shell clam). Chesapeake Sci. 13(suppl.): S182-S184.

RAO, C. R.
1958. Some statistical methods for comparison of growth curves. Biometrics 14:1-17.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

ROPES, J. W., AND A. P. STICKNEY.
1965. Reproductive cycle of *Mya arenaria* in New England. Biol. Bull. (Woods Hole) 128:315-327.

ROFF, D. A.
1980. A motion for the retirement of the von Bertalanffy function. Can. J. Fish. Aquat. Sci. 37:127-129.

SAMEOTO, D. D.
1972. Yearly respiration rate and estimated energy budget for *Sagitta elegans*. J. Fish. Res. Board Can. 29: 987-996.

SCHNUTE, J., AND D. FOURNIER.
1980. A new approach to length-frequency analysis: Growth structure. Can. J. Fish. Aquat. Sci. 37:1337-1351.

SHOREY, W. K.
1973. Macrobenthic ecology of a sawdust-bearing substrate in the Penobscot River estuary (Maine). J. Fish. Res. Board Can. 30:493-497.

SHUSTER, C. N.
1951. On the formation of mid-season checks in the shell of *Mya*. [Abstr.] Anat. Rec. 111:543.

SWAN, E. F.
1952. The growth of the clam *Mya arenaria* as affected by the substratum. Ecology 33:530-534.

TESCH, F. W.
1971. Age and growth. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 98-130. Blackwell Sci. Publ., Oxford.

THOMAS, M. L. H.
1978. Comparison of oiled and unoiled intertidal communities in Chedabucto Bay, Nova Scotia. J. Fish. Res. Board Can. 35:707-716.

TURNER, H. J., JR.
1948. Report on investigations of the propagation of the soft-shell clam, *Mya arenaria*. Rep. Invest. Shellfish. Mass. 1:3-9.

WELCH, W. R.
1981. Monthly and annual means of sea surface temperature: Boothbay Harbor, Maine 1905 through 1980. Maine Dep. Mar. Resour., Res. Ref. Doc. 81/8.

WILTON, M. H., AND H. I. WILTON.
1929. Conditions affecting the growth of the soft shell clam, *Mya arenaria* L. Contrib. Can. Biol. Fish. 4:81-93.

APPENDIX TABLE 1.—The age (yr), length ±1 standard deviation (mm), and percent of sample in each age class. Percentages may not total 100 due to roundoff or exclusion of some outliers from the analysis. Sample size is given in parentheses. — = undefined.

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	Quonochontaug Pond-2 (146)			Saugatucket River (140)		
Deer Isle (318)			2.15	33.7±2.7	41	2.0	29.0±1.3	2
3.0	25.7±1.9	4	3.15	41.6±2.0	28	2.6	33.8±0.9	5
4.0	31.2±1.1	7	4.15	49.0±1.3	6	3.0	37.6±1.6	9
5.0	35.2±1.3	21	5.15	55.1±1.8	6	3.8	43.3±2.2	42
6.0	39.2±1.3	18	6.15	60.2±1.0	4	4.8	48.9±1.5	7
7.0	42.1±1.1	9	7.15	65.8±1.3	6	5.8	52.8±1.1	12
8.0	44.6±1.0	10	8.15	70.5±0.8	4	7.0	56.1±0.7	6
9.0	47.8±1.0	12	9.15	73.5±0.8	3	8.0	60.0±1.2	6
10.0	51.5±1.0	9	10.15	79.0±1.1	4	9.0	64.5±1.2	3
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)			Big Annemessex River (177)			Robinston (190)		
1.15	27.6±2.9	24	1.33	57.0±1.3	14	3.67	37.9±1.6	8
2.15	34.8±2.0	31	1.80	60.9±1.8	30	4.67	42.5±1.6	16
3.15	42.4±1.7	19	2.33	68.8±2.0	33	5.67	47.2±1.6	41
4.15	48.2±2.5	11	2.80	73.7±0.8	4	6.67	51.7±1.0	20
6.15	57.1±1.4	8	3.33	77.2±1.3	7	7.67	54.6±0.9	7
7.15	62.5±1.0	6	4.33	86.8±1.5	2	8.67	57.0±1.2	4
New Bedford (180)			Stockton Harbor (164)			Tangier Sound (166)		
1.85	32.0±1.0	0.5	3.0	31.0±1.8	2	1.33	54.6±2.3	36
2.85	43.7±1.2	3	4.0	38.2±1.8	2	1.80	62.0±1.6	26
3.56	48.3±1.6	8	5.0	44.8±1.4	11	2.33	67.9±1.2	13
3.85	51.2±0.8	15	6.0	49.2±1.1	13	2.80	73.4±1.3	11
4.56	53.9±0.9	16	7.0	54.1±1.5	17	3.33	78.2±0.9	3
4.85	56.2±0.9	21	8.0	58.2±1.2	21	3.80	81.6±0.8	1
5.56	58.9±1.2	16	9.0	62.8±1.3	13	4.33	86.2±0.7	2
5.85	61.2±0.8	11	10.0	66.5±1.4	11			
6.85	64.4±0.9	6	11.0	70.3±1.2	3	Raritan Bay (200)		
7.85	69.0±0.6	3	12.0	75.0±1.3	5	1.33	30.4±0.8	3
Winnapaug Pond (229)			Wickford (203)			1.67	36.4±1.8	23
0.9	24.2±1.6	3	0.20	7.0 —	0.5	2.33	40.2±1.7	39
1.5	31.5±1.0	2	2.00	37.3±1.1	2	2.67	43.8±1.6	25
1.9	37.4±1.2	5	2.67	48.7±1.4	4	3.33	47.4±0.8	10
2.5	41.4±1.2	7	3.00	53.9±1.4	10			
2.9	46.2±1.3	14	3.80	60.4±1.8	18	East Greenwich Cove (192)		
3.5	50.6±1.8	24	4.80	68.1±2.5	36	1.0	20.8±3.5	30
4.5	56.0±1.6	29	5.80	75.1±1.8	13	2.0	30.8±1.0	9
5.5	60.5±1.2	8	6.00	80.2±1.1	7	3.0	38.4±2.8	49
6.5	64.1±1.4	4	7.00	84.7±0.9	2	4.0	45.0±1.5	11
7.5	67.2±0.7	4	8.00	88.5±0.6	2	5.0	50.9±1.1	3