

# A Quantification of some Aspects of Growth in the Bottom-Feeding Bivalve *Macoma nasuta*

BY

VINCENT F. GALLUCCI

Center for Quantitative Science in Forestry, Fisheries, and Wildlife  
and The College of Fisheries, University of Washington, Seattle, Washington 98195

AND

J. HYLLEBERG

Zoologisk Institut, University of Aarhus, Denmark

(6 Text figures)

## INTRODUCTION

DESPITE THE LARGE NUMBER of studies on the feeding biology of deposit-feeding bivalves, questions concerning the dependence of growth upon sediment composition and the application of allometric relations for describing growth remain to be answered. To better understand the nutritional basis for growth of deposit-feeders, HYLLEBERG & GALLUCCI (1975) studied the feeding selectivity and growth of *Macoma nasuta* (Conrad, 1837), a deposit-feeding intertidal bivalve of the west coast of North America (POHLO, 1973).

NEWELL (1965) worked with *Macoma balthica* (Linnaeus, 1758) and demonstrated that the animals' energetics are highly dependent upon the microorganisms which coat the surface of sand particles. *Macoma nasuta* is also capable of removing microorganisms from particle surfaces. A silt-clay environment is considered to be nutritionally richer because a given weight of fine silt-clay would have a greater surface area and thus microorganism content than that of a coarse sand. In addition to microorganisms, detritus is selected for and makes, at its early stage of decomposition, some contribution to the nutrition of *M. nasuta* (HYLLEBERG & GALLUCCI, 1975). The significance of suspension feeding is incompletely known in

tellinaceans, although the possibility is often mentioned, e. g., in BRAFIELD & NEWELL (1961). In *M. nasuta* the significance of suspension feeding was not determined (HYLLEBERG & GALLUCCI, *op. cit.*).

There is an extensive literature on growth in bivalves, some of which is quantified in the form of various types of mathematical growth models. Analytical growth models usually entail at least 2 parameters, a maximum body size and a growth constant. If growth is noted by a linear measurement (e. g., length) the maximum size would be  $L_{\infty}$  and the corresponding weight  $W_{\infty}$ . Growth rates in time could then be  $dl(t)/dt$  and  $dw(t)/dt$  and the growth constant would be  $k$ . The well known von Bertalanffy model uses maximum sizes, growth rate and a third parameter  $t_0$  (VON BERTALANFFY, 1938) and other more elaborate models contain additional parameters (SOUTHWARD & CHAPMAN, 1965; FLETCHER, 1974). However, the estimation and testing of parameters must be done with care to avoid problems associated with the fact that parameters may not be independent of each other (GALLUCCI & QUINN, in manuscript).

This paper reports on comparative growth studies of *Macoma nasuta* in silt-clay and medium coarse sand at approximately the 0.0 tide line. Concurrent studies were done in the laboratory (HYLLEBERG & GALLUCCI, 1975) where the proportion of the contribution to growth during different modes of feeding could be controlled. In contrast to analytical growth models, time ( $t$ ) is not the independ-

<sup>1</sup> Contribution No. 434, College of Fisheries, University of Washington, Seattle, Washington



ent parameter. Instead, the data are reported as weight (ash free)  $w(t)$  as a function of length  $l(t)$ . The empirical, allometric model of the form  $w = al^b$  shows that the maximum length is a critical parameter, as is the growth rate  $q = dw/dl$ .

## METHODS

The field experiments were done in Garrison Bay, a small bay of San Juan Island in the San Juan Archipelago, Washington (Figure 1). The bay is approximately 3 km

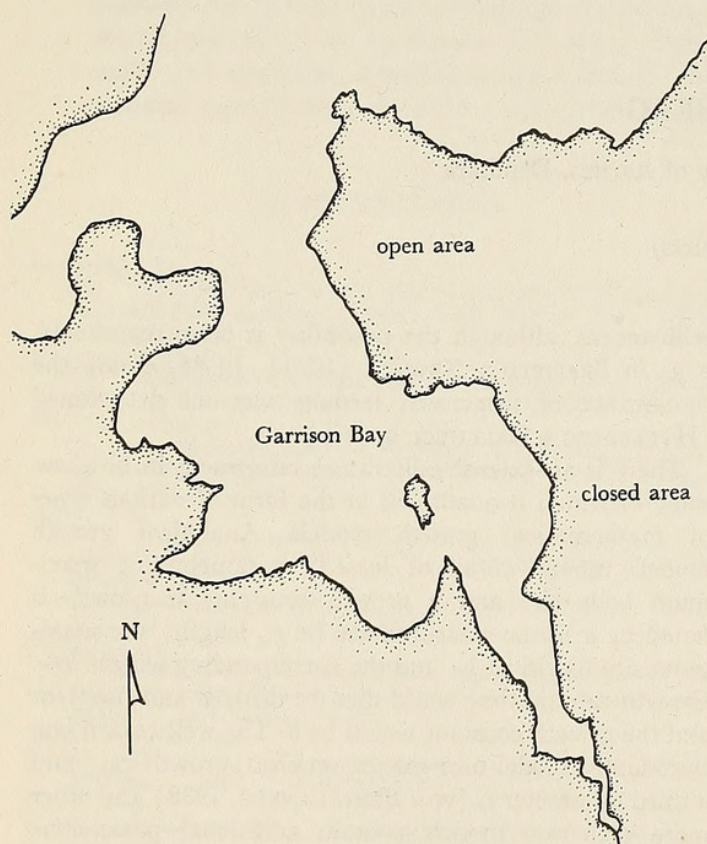


Figure 1

Garrison Bay, San Juan Island, Washington, USA

long and 0.8 km wide with a classic sediment profile: fine silt and clay substrate at the closed end where the anaerobic layer is very near the surface and coarse sand at the open end. The experiment to evaluate growth consisted of burying 9 measured *Macoma nasuta* in the open area of the bay and 9 in the closed area. In each set of 9, 3 were juvenile (pre-reproductive), 3 were in the mid-size range

and 3 had sizes near  $L_{\infty}$ . The 9 clams in the closed area were selected from about 60 that were dug until the appropriate sizes were found. They were all dug from a region adjacent to where the 9 were buried. A similar explanation applies to the open area. Each clam's length was measured and the clam was placed in a plastic 1-liter capacity container which was cut at the sides and bottom and covered with a 1 mm window screen to allow water

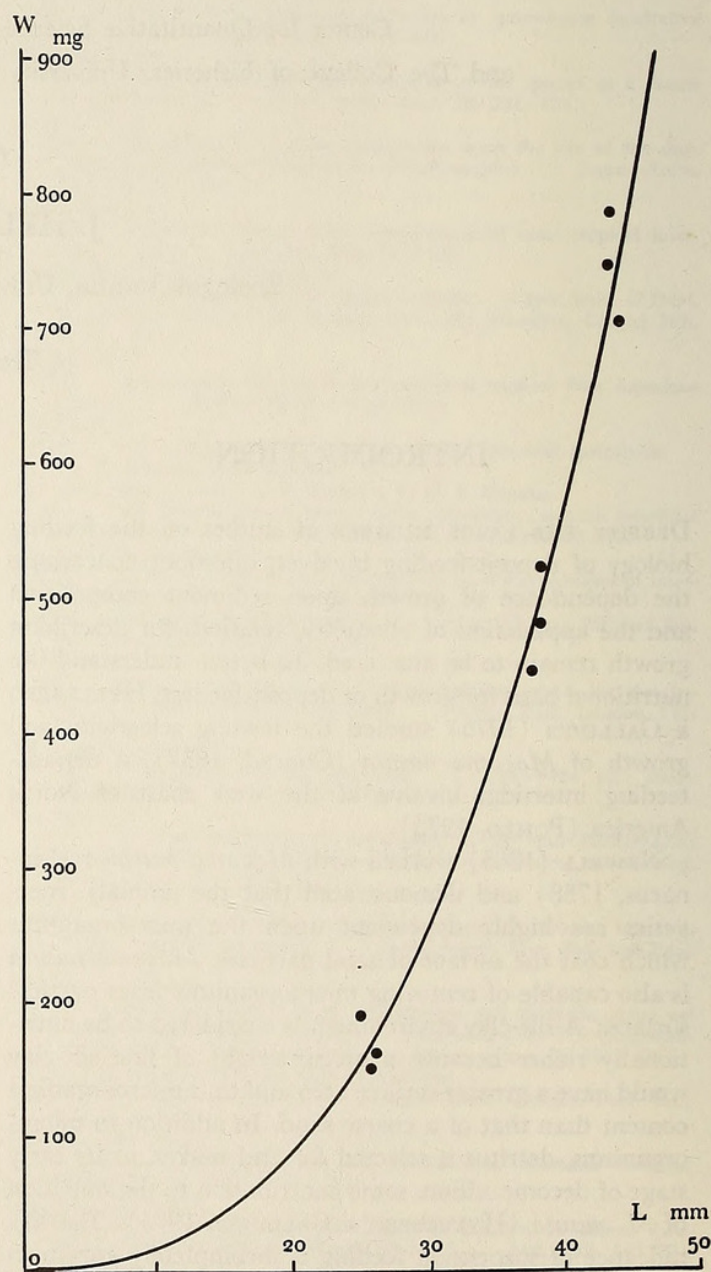


Figure 2

Data Points and the Curve  $w = al^b$  from the Open Area Field Experiment (FO)



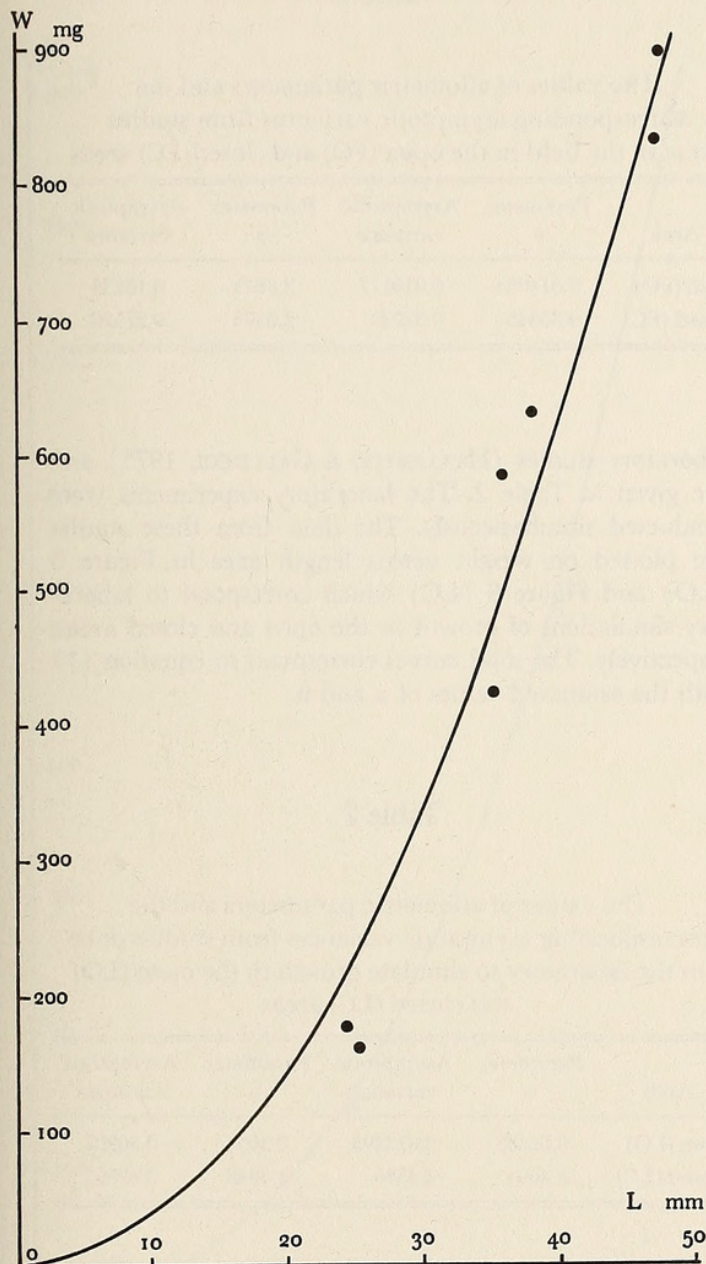


Figure 3

Data Points and the Curve  $w = a l^b$  from the Closed Area  
Field Experiment (FC)

transport across the boundary. Each container was filled with sediment from an adjacent location and buried flush to the sediment. All of the 9 containers were buried adjacent to each other and parallel to the water line in areas that visually appeared similar with respect to living and decaying algal cover (*Enteromorpha intestinalis* and

Ulvoids). Therefore, differences in exposure to organics would largely be a consequence of sediment differences. Since sediment in the containers was sieved to remove possible competitors, any competition was due to epifaunal colonizers such as *Transennella tantilla* (Gould, 1853). After 40 days of growth, starting in mid-July, 1974, the clams were dug up and the lengths measured. Shell length, the longest possible postero-anterior distance, was measured to within 0.1 mm with a vernier caliper. The ashfree weights of the animals that had been growing for 40 days were found by drying animal tissue for at least 24 hours at 80° C and burning at 550° C for 24 hours. It was determined that *M. nasuta* valves contain no more than 5 mg of organic matter. Figures 2 and 3 contain the data points from field experiments on weight  $w(t)$  versus length  $l(t)$  axes for the open and closed areas, respectively.

The differences in the particle size composition of the growing regions were quantified. Two sediment cores each were taken from the open and closed areas of the bay. The cores were dried at 100° C for 4 hours; the dried sediment was picked free of large organics, put on an automatic shaker and passed through a series of sieves of mesh sizes: 1.980, 0.495, 0.246, 0.124, 0.063 mm. The sediment retained by each sieve and that passed through the 0.063 was weighed to get the percent of sediment in each size range. The averaged cumulative percentage weight curves of the 2 sediments are similar in shape but the closed end area always contains a silt-clay component at least 2 times larger by weight than the open end.

The differences in the organic content of the 2 areas was found by loss on burning. Organic content of the sediment was determined by taking a sediment core from each area of the bay, freezing it for 4 days, removing the top 4 cm from the cores, drying and burning as above. Loss on burning was calculated as loss/mg dry weight of sediment. Sediment from the closed area contained twice as much combustible organics as sediment from the open area. Presumably much of the difference is due to there being a greater number of microorganisms and detritus in the sediment from the closed area of the bay.

Salinity in the bay is relatively constant at about 28 to 30‰ during the primary growing time, but at specific "run-off areas" the salinity of the water that fills a hole dug in the intertidal zone may be as low as 16‰. Neither growth study was in such an area. Water temperature in the open area is about 12° C and on warm sunny days it is about 2° C higher in the closed area.

In late August an estimate of the average bivalve density (*Macoma nasuta*, *M. inquinata*, *M. inconspicua* (*balthica*), *Protothaca staminea*, and other large suspension feeders) in each area of the bay in the vicinity of the growing site was found by digging a 1.5 m x 25 cm x 60 cm



trench and sieving all sediment through a mesh size of 6 mm, thus recovering most of the small size classes. The *M. nasuta* density in the open and closed areas was approximately the same and, although the size-frequency distributions (Figure 4) are translated horizontally, they are similar.

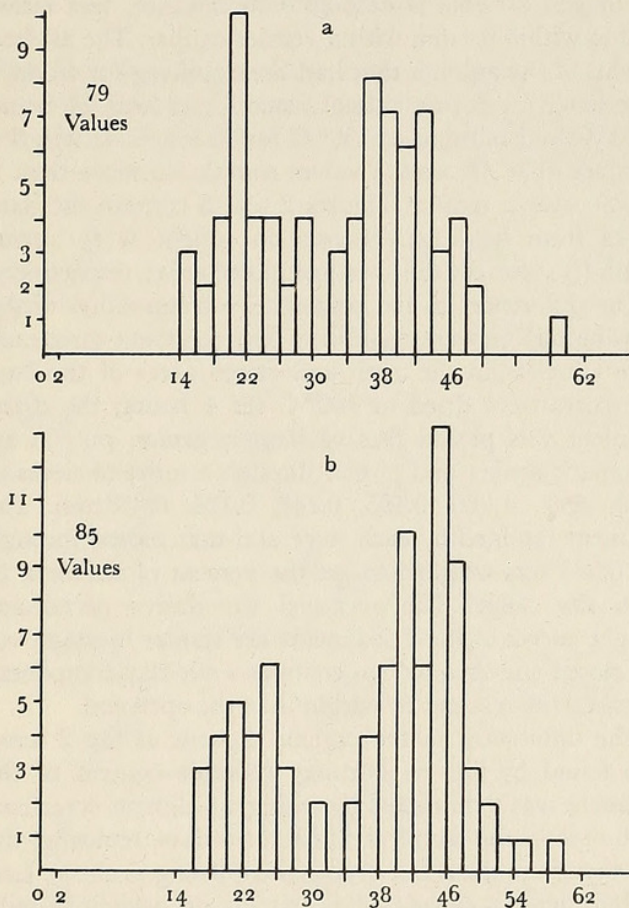


Figure 4

- a. Size-frequency Curve of *Macoma nasuta* from the Open Area  
b. Size-frequency Curve of *Macoma nasuta* from the Closed Area

Predicted growth curves of the form

$$w = a l^b \quad (1)$$

were fitted to the field data plotted in Figures 2 and 3 and are the solid curves drawn in these figures. The allometric parameters,  $a$  and  $b$ , of the curves are in Table 1. These parameters for the field experiments in the open (FO) and the closed areas (FC) were statistically compared to each other. Similar statistical comparisons of parameters  $a$  and  $b$  were done with the growth data from compatible

Table 1

The values of allometric parameters and the corresponding asymptotic variances from studies done in the field in the open (FO) and closed (FC) areas

Area	Parameter $a$	Asymptotic variance	Parameter $b$	Asymptotic variance
Open (FO)	0.014084	0.010117	2.8655	0.19233
Closed (FC)	0.30845	0.32049	2.0495	0.27526

laboratory studies (HYLLEBERG & GALLUCCI, 1975) and are given in Table 2. The laboratory experiments were conducted simultaneously. The data from these studies are plotted on weight versus length axes in Figure 5 (LO) and Figure 6 (LC) which correspond to laboratory simulations of growth in the open and closed areas, respectively. The solid curves correspond to equation (1) with the estimated values of  $a$  and  $b$ .

Table 2

The values of allometric parameters and the corresponding asymptotic variances from studies done in the laboratory to simulate growth in the open (LO) and closed (LC) areas

Area	Parameter $a$	Asymptotic variance	Parameter $b$	Asymptotic variance
Open (LO)	0.06388	0.073293	2.4654	0.30307
Closed (LC)	1.4604	4.4586	1.5948	0.82595

The allometric parameters  $a$  and  $b$  for the laboratory and field experiments were also compared. The test of comparison is Rao's Chi-Square Test (RAO, 1973: 389 to 391).

The non-linear equation (1) was fit using the least squares BMD X85 program on a CDC 6400. This particular equation was used for 2 reasons: the experimental data are clearly of this form with no apparent inflection or turning points and because the equation, known as the allometric relation, has found wide application in growth studies of many organisms (BEVERTON & HOLT, 1957; ALDRICH, 1974).



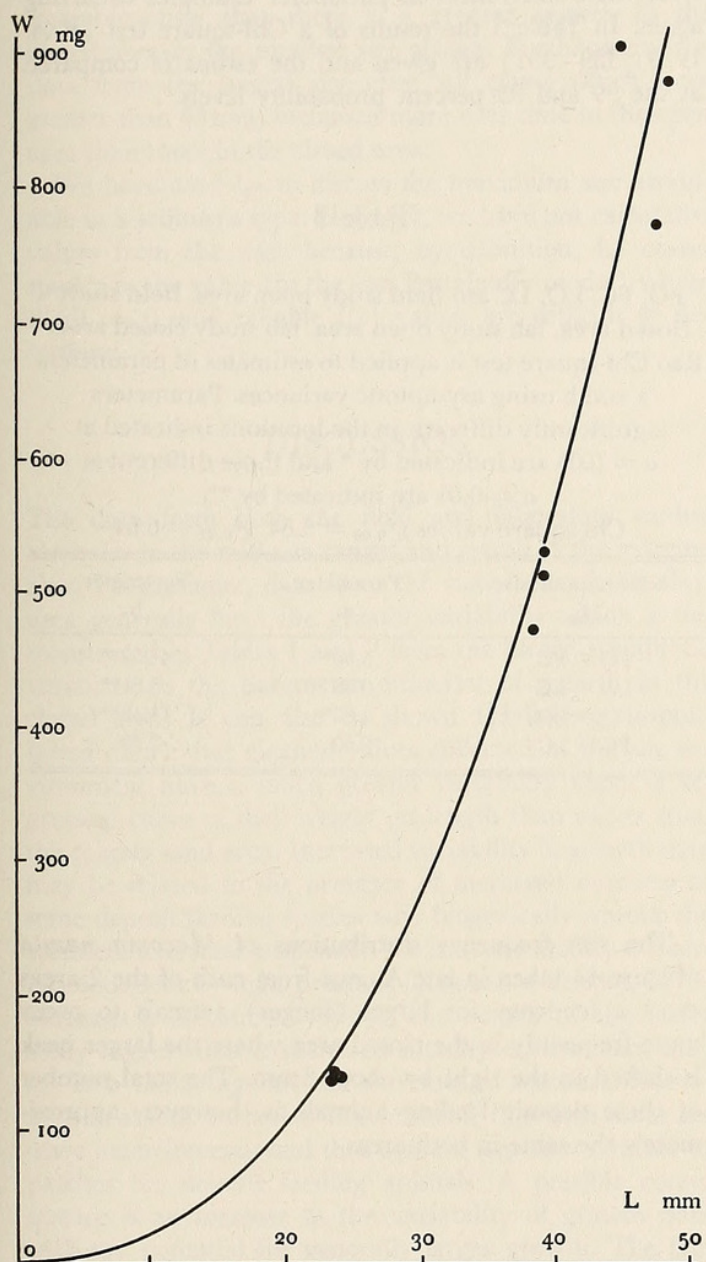


Figure 5

Data Points and the Curve  $w = a l^b$  from the Open Area  
Laboratory Experiment (LO)

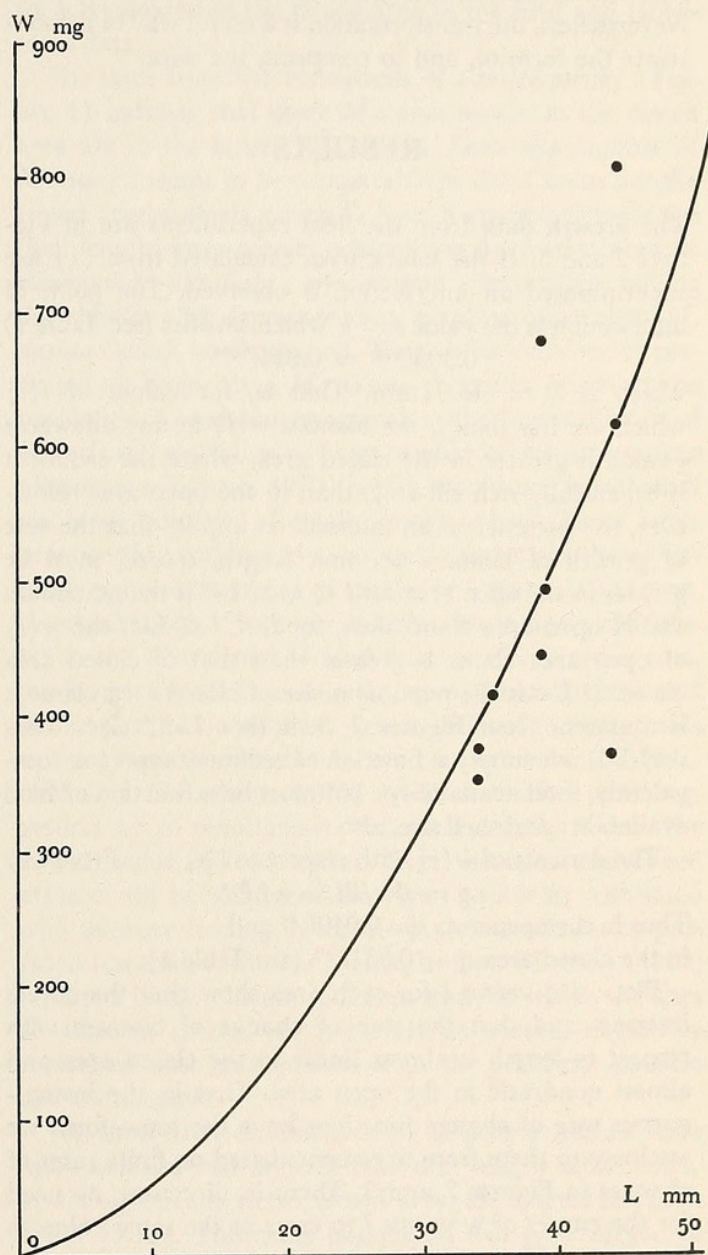


Figure 6

Data Points and the Curve  $w = a l^b$  from the Closed Area  
Laboratory Experiment (LC)

It is well known that the parameters  $a$  and  $b$  may be estimated from a log - log transformation of (1) and linear regression. Parameter  $a$  would correspond to the verti-

cal intercept and  $b$  to the slope. This method of estimating  $a$  and  $b$  is common in early work but is now unacceptable due to the bias which may be introduced by the trans-



formation (GLASS, 1967; ZAR, 1968). Non-linear regression is preferable in this age of calculators and computers. Nevertheless, the transformation is a useful way to demonstrate the form of, and to compress, the data.

## RESULTS

The growth data from the field experiments are in Figures 2 and 3. If the solid curves calculated from (1) are superimposed an intersection is observed. The point of intersection is the value  $l = l_1$  which satisfies (see Table 1)

$$0.308l^{2.050} = 0.014l^{2.866}$$

which is  $l_1 = 43.94\text{mm}$ . That is, for values of  $l(t)$  which are less than  $l_1$  the biomass  $w(l)$  at any allowable  $l$ -value is greater in the closed area, where the sediment is organically rich silt-clay, than in the open area. However, the presence of an intersection implies that the rate of growth of biomass per unit length,  $dw/dl$ , must be greater in the open area for  $l < l_1$ . If  $L_{\infty}^o$  is the maximum size of open area clams then, for  $l_1 < l < L_{\infty}^o$ , the  $w(l)$  of open area clams is greater than that of closed area clams. If  $L_{\infty}^c$  is the maximum size of closed area clams it is apparent from Figures 2, 3, 4 that  $L_{\infty}^c > L_{\infty}^o$ . Thus  $dw/dl$  is not simply a function of sediment type (or equivalently, food availability) but must be a function of food availability and shell size, also.

The derivate of  $w(t)$  with respect to  $l(t)$  is  $q$ . From (1)

$$q = dw/dl = a bl^{b-1}$$

Thus in the open area  $q = 0.040l^{1.87}$  and in the closed area  $q = 0.631l^{1.05}$  (see Table 1).

Plots of  $q$  versus  $l$  for each area show that the curves intersect and that the rate of change of biomass with respect to length is almost linear in the closed area and almost quadratic in the open area. That is, the instantaneous rate of change functions have the same form we attribute to them from arguments based on finite rates of changes in Figures 2 and 3. There is, of course, no need for the curves of  $w$  versus  $l$  to cross at the same value as the curves of  $q$  versus  $l$ .

Curves fit from laboratory experiments (HYLLEBERG & GALLUCCI, 1975) using the same sediment types show the same qualitative behavior. The intersection of the curves in Figures 5 and 6 occurs at the  $l = l_2$  which satisfies (see Table 2)

$$0.064l^{2.465} = 1.460l^{1.595}$$

which is  $l_2 = 36.40\text{mm}$ . Thus the laboratory studies show that closed area clams have a greater biomass than open area clams for  $l < l_2$ . This result is compatible with, but less than the values found in the field study.

The comparison of the growth in different sediments in the field and in the laboratory is of more value when a

quantitative statement can be made about the probability of these differences in parameter estimates occurring again. In Table 3 the results of a Chi-square test (RAO, 1973: 389 - 391) are given and the estimates compared at the 99 and 95 percent probability levels.

Table 3

FO, FC, LO, LC are field study open area, field study closed area, lab study open area, lab study closed area. Rao Chi-square test is applied to estimates of parameters  $a$  and  $b$  using asymptotic variances. Parameters significantly different in the locations indicated at  $\alpha = 0.05$  are indicated by \* and those different at  $\alpha = 0.01$  are indicated by \*\*.

Chi square values  $\chi^2_{0.05} = 3.84$ ,  $\chi^2_{0.01} = 6.64$

Null hypothesis $H_0$	Parameter $a$	Parameter $b$
FO = FC	5.90*	44.59**
LO = LC	0.88	8.81**
FO = LO	4.08*	11.18**
FC = LC	0.60	2.39

The size frequency distributions of *Macoma nasuta* (Figure 4) taken in late August from each of the 2 areas show a tendency for larger (longer) animals to occur more frequently in the closed area where the larger peak is shifted to the right by about 3mm. The total number of these deposit feeding animals is, however, approximately the same in both areas.

Table 4

Average change in length  $\Delta l$  over time for clams in field experiments in the open (FO) and closed (FC) areas

Area	Size range		
	smallest	mid	largest
Closed (FC)	4.1	0.40	0.15
Open (FO)	2.7	0.70	0.60



The data on changes in length ( $\Delta l$ ) over the 40 day growing period in the field are given in Table 4 and show unambiguously that there is a greater growth in the closed area in the smallest size classes. Furthermore, the data from the largest size class, all clams which were greater than 43 mm, increased more over time in the open area than those in the closed area.

We have used  $L_{\infty}$  to discuss the maximum size attainable in a sediment type. However, we have not calculated values from the data because, by definition,  $L_{\infty}$  corresponds to the value (in the von Bertalanffy model) where  $dl/dt = 0$ , and reliable  $l(t)$  values are difficult to determine.

## DISCUSSION

The data from both the field and laboratory studies are noisy in the mid-size ranges and less so at the extreme sizes. Furthermore, data from the richer closed, silt-clay, area generally have the greater variability which is demonstrated in Tables 1 and 2 from the larger asymptotic variances in the parameter estimates of growth in the closed area. It can also be shown (Hylleberg, unpublished data) that cleaned valves collected in the silt environment have a much greater variability about a regression curve of shell weight on length than valves from the coarser sand area. Increased variability in growth data may be related to the presence of increased numbers of some deposit feeding species who biogenically rework the sediment and some suspension feeders who modify the surface sediment by their presence (RHODES & YOUNG, 1970; SCHERBA & GALLUCCI, 1976). The results of the latter study suggest that a sheltered silt-clay environment may act as a buffer against the extremes of seasonal fluctuations in abiotic variables. It is probable that such areas are more heterogeneous and thus contain a greater number of patches for deposit feeding animals. A possible consequence is an increase in the variability of growth data with the potential for generally larger growth. The fact that the curves in Figures 2, 3 and 5, 6 are qualitatively similar with the intersections occurring in comparable size ranges is further evidence that the reported growth characteristics are not artifacts.

The exponent  $b$  in both laboratory and field studies is significantly different at  $\alpha = 0.01$  when values for the open and closed areas are compared. Although the coefficient  $a$  in the laboratory study is not significantly different at either  $\alpha$  level (in comparison of open and closed areas), a significant difference at the  $\alpha = 0.05$  level is found between the parameter values estimated from the 2 areas in the field study (Table 3). The results from tests

of significance are certainly influenced by the above noted higher asymptotic variances associated with the parameter  $a$ , evaluated in the closed area in the field and laboratory data.

The data from the histograms of size-frequency (Figure 4) indicate that more *Macoma nasuta* in the closed area are in the largest size classes. Since the number of *M. nasuta* seems to be comparable in the 2 areas but the closed area animals generally have a greater biomass per shell length, intra-species competition for food cannot be eliminated. Similarly, inter-species competition among polychaetes and deposit-feeding bivalves other than *M. nasuta* cannot be eliminated. There is no evidence of predation on larger sized *M. nasuta*. There is, however, the possibility of predation on animals in the 0-year class or of an indirect mortality such as trophic group amensalism (RHODES & YOUNG, 1970) which would not reveal itself via large amounts of small, empty valves. These latter processes are considered as probable factors in the occurrence or non-occurrence of species in a patch (GALLUCCI, in preparation). Since our calculations indicate differences in the abundance of food items in the 2 areas, i. e., predominance of diatoms in the open, versus bacteria and detritus in the closed area, we are inclined to suggest this as an explanation for the observed growth behavior. HYLLEBERG & GALLUCCI (1975) tried to confirm this suggestion by a simultaneous laboratory study where the growth value of food sources from the open and closed areas could be analyzed. However, problems associated with selective feeding by sorting in the mantle cavity provided less than definitive results. In fact, MAURER (1969) reports a bivalve-length-sediment study in which the sizes of different species are positively correlated, negatively correlated and uncorrelated with the sediment particle size distribution.

We show that deposit feeding *Macoma nasuta* have more biomass and add biomass/unit length more slowly in the organically richer closed area, for lengths less than about 43 mm. This same population will grow larger on the average than open area clams and, for lengths greater than about 43 mm, biomass per unit length is added faster than for the open area clams. The data in Table 4 also show a decreased rate (with respect to time) of growth for large clams from the closed area as compared to the open area. These results indicate an environmentally related dependence between maximum size and  $dw/dl$ . Growth parameters  $L_{\infty}$  and  $W_{\infty}$  are often estimated from each other using the allometric relation and  $L_{\infty}$  is often estimated by fitting the von Bertalanffy growth law (BEVERTON & HOLT, 1957). However, it does not necessarily follow that  $dw/dl$  and  $dl/dt$  are always related to each other in



a straightforward way analogous to the mathematical relationship of the chain rule derivative of  $w(t)$  with respect to  $t$ . Despite this, comparisons are made of populations' growth or of environments' capacity for growth using some of these quantifiable parameters and calculating the others. Our results indicate that, at least for deposit feeding bivalves, the biological relationships may be more complicated. The inter-relationships suggested here are usually masked in biomass versus time or length versus time studies, or both.

The allometric relation (1) between biomass and length is a natural function to use to describe such data. The exponent values are between 2 and 3 as expected from arguments based on the relationships between biomass, volume and linear dimensions and from previous studies on marine fin fish (BEVERTON & HOLT, 1957). Furthermore, despite variability in the mid-range, the data also have this polynomial form.

The estimated parameters  $a$  and  $b$  are, subject to the preceding, indicators of the conditions of growth the different populations experience. If  $a$  and  $b$  could be estimated from growth over a single year, anomalies of that year's growing conditions might govern the estimates. However,  $a$  and  $b$  are estimated from clams growing from 1 to about 6 years, so anomalies tend to cancel (trends would not cancel). Since *Macoma nasuta* is a dominant animal in the mud flat community of Garrison Bay (GALLUCCI, in preparation) the parameters  $a$  and  $b$  may be considered as community indices whose stability is quantifiable.

## SUMMARY

In this report we demonstrate the applicability of the allometric relation between biomass and length in *Macoma nasuta*, a deposit feeding bivalve, and statistically test the null hypothesis of no difference in biomass versus length curves for a population growing in a rich silt-clay environment and a population growing in a medium-coarse sand environment. The allometric parameters are shown to be statistically different, establishing that there is a difference in the way biomass increases with respect to valve length in each environment.

The curves of biomass versus length in the 2 environments intersect at 43 mm. Biomass values in the richer environment are greater for lengths less than 43 mm. The biomass values are greater in the sand environment at lengths between 43 mm and the maximum length (approximately 50 mm). Rates of increase of biomass with

respect to length are indicated. A size-frequency study demonstrates that there is a greater number of larger bivalves in the richer environment.

Simultaneous studies done in the laboratory (HYLLEBERG & GALLUCCI, 1975) yield similar growth curves and generally confirm the field results.

Both field and laboratory results point to increased variability in silty environments which seems to translate to a greater heterogeneity with meaningful implications for understanding sediment inhabiting animals.

## ACKNOWLEDGMENTS

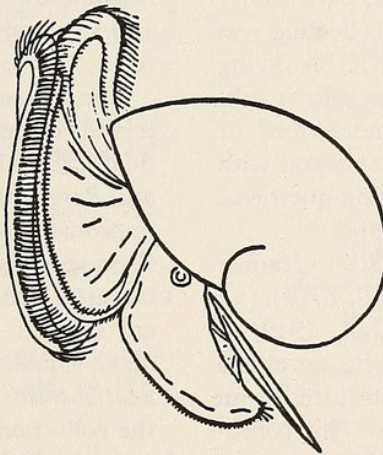
We are grateful to A. O. D. Willows, Director of the Friday Harbor Marine Laboratories, for providing excellent research facilities. The cooperation of C. E. Lindsay of the Washington Department of Fisheries and S. J. Zachwieja of the National Park Service in establishing the research areas is gratefully recognized. We wish to thank T. Quinn for his assistance with the computer programming of the polynomial parameter estimates and the test of statistical significance. T. Quinn and B. J. Gallucci critically read the paper. J. Wood provided outstanding assistance with the field work and A. Siebert made early contributions in the field work. Financial support from the Danish Research Council to J. Hylleberg and from the Washington Sea Grant Program (SG 61-8227) to V. Gallucci is gratefully acknowledged.

## Literature Cited

- ALDRICH, J.  
1974. Allometric studies on energy relationships in the spider crab *Libinia emarginata* (Leach). *Biol. Bull.* 147: 257-273
- BEVERTON, R. & S. HOLT  
1957. On the dynamics of exploited fish populations. *Fish Invest.*, Ser. II: 19. Her Majesty's Stationery Office, London
- BERTALANFFY, LUDWIG VON  
1938. A quantitative theory of organic growth (inquiries on growth laws. II.). *Human Biol.* 10 (2): 181-213
- BRADFELD, A. W. & G. E. NEWELL  
1961. The behaviour of *Macoma balthica*. *Journ. Mar. Biol. Assoc. U. K.* 41: 81-87
- FLETCHER, R.  
1974. The quadratic law of damped exponential growth. *Bio-metrics* 30: 111-124
- GALLUCCI, VINCENT F. & T. QUINN  
(in prep.) Remarks on the use and misuse of a growth model.
- GLASS, N.  
1967. A technique for fitting nonlinear models to biological data. *Ecology* 48: 1010-1013
- HYLLEBERG, J. & VINCENT F. GALLUCCI  
1975. Selectivity in feeding by the deposit-feeding bivalve *Macoma nasuta*. *Mar. Biol.* 32 (2): 167-178
- MAURER, DON  
1969. Pelecypod-sediment association in Tomales Bay, California. *The Veliger* 11 (3): 243-249; 1 text fig. (1 January 1969)



- NEWELL, RICHARD CHARLES  
1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. *Proc. Zool. Soc. London* 144: 25 - 45
- POHLO, ROSS H.  
1973. Feeding and associated functional morphology in *Tagelus californianus* and *Florimetus obesa* (Bivalvia: Tellinacea). *Malacologia* 12: 1 - 11
- RAO, C.  
1973. Linear statistical inference and its applications. John Wiley and Sons, Inc., New York. 625 pp.
- RHODES, D. & D. YOUNG  
1970. The influence of deposit feeding organisms on sediment stability and community structure. *Journ. Mar. Res.* 28: 150 - 178
- SCHERBA, S. & VINCENT F. GALLUCCI  
1976. The application of systematic sampling to a study of infauna variation in a soft substrate intertidal environment. *The Fishery Bull.*
- SOUTHWARD, G. & D. CHAPMAN  
1965. Utilization of Pacific halibut stocks: study of Bertalanffy's growth equation. *Int. Pacif. Hal. Comm. Rep.* 39
- ZAR, J.  
1968. Calculation and miscalculation of the allometric equation as a model in biological data. *BioScience* 18: 1118 - 1120







Gallucci, Vincent F. and Hylleberg, J. 1976. "A QUANTIFICATION OF SOME ASPECTS OF GROWTH IN THE DEPOSIT FEEDING BIVALVE MACOMA-NASUTA." *The veliger* 19, 59–67.

**View This Item Online:** <https://www.biodiversitylibrary.org/item/134154>

**Permalink:** <https://www.biodiversitylibrary.org/partpdf/93657>

**Holding Institution**

Smithsonian Libraries and Archives

**Sponsored by**

Biodiversity Heritage Library

**Copyright & Reuse**

Copyright Status: In Copyright. Digitized with the permission of the rights holder.

Rights Holder: California Malacozoological Society

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://www.biodiversitylibrary.org/permissions/>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.