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Relationships between the bivalve Macoma balthica and bacteria in intertidal sediments: Minas Basin, Bay of Fundy

by Verena Tunnicliffe[1,2] and Michael J. Risk[1]

ABSTRACT

The extensive intertidal flats of the Minas Basin, Bay of Fundy, support some of the highest population densities of Macoma balthica ever recorded. Densities of Macoma are positively correlated with density of bacteria in the sediment; correlations with tidal elevation and organic carbon content of the sediment are not significant. Macoma density appears to be related to the amount of fine material present in the sediment. Although Macoma feeds on the bacteria within the sediment, it must supplement its diet by suspension-feeding during high tide in order to acquire sufficient protein.

1. Introduction

The Minas Basin, the most easterly extension of the Bay of Fundy, is characterized by turbid water, low wave action, and tidal ranges of up to 17 m (Bousfield and Leim, 1959). The vast intertidal flats, in some cases more than 4 km wide, support a high-density, low-diversity assemblage of benthic invertebrates, mostly deposit-feeders. This intertidal assemblage is dominated by the tellinid bivalve Macoma balthica and the amphipod Corophium volutator, with scattered occurrences of Mya arenaria, Neanthes virens, Arenicola marina and Hydrobia ulvae (Craig and Risk, 1975), and is therefore very similar to Petersen's subtidal "Macoma balthica Community" (Petersen, 1913).

Macoma balthica has a long incurrent siphon and a short excurrent siphon. When deposit-feeding, the incurrent siphon moves about on the surface of the water-saturated sediment, sucking up the topmost layer of flocculent material (Bubnova, 1972). Rejected sediment is ejected from the incurrent siphon as loose pseudofeces; ingested sediment passes through the gut and is voided as discoidal fecal pellets. Continued deposit-feeding by Macoma results in each clam being surrounded by a shallow depression about 5 cm in diameter. Macoma-bearing flats may be recognized from a distance, as they exhibit a characteristic dimpled surface.

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The *Macoma* zone in the Minas Basin is approximately 350 m wide, and the maximum recorded density of adult clams in this study is 3500/m². To the best of our knowledge, this is the highest population density of *Macoma balthica* ever recorded from North America, and is exceeded only by a density of 6000/m² from the Mersey Estuary (Fraser, 1932).

The importance of bacteria in converting relatively refractory plant and animal carbohydrate (lignin, cellulose, chitin) into high-protein bacterial biomass, suitable for ingestion by deposit-feeders, has been emphasized by several previous authors. MacGinitie (1932), ZoBell and Feltham (1943), Wood (1965), Newell (1965) and Gosselink and Kirby (1974) believe that volumetrically bacteria may prove to be an important food source for macroorganisms. Hargrave (1970) and Dale (1974), on the other hand, feel the contribution may be insignificant. Marzolf (1965) found that the abundance of a fresh water burrowing amphipod correlated highly with microbial density, as well as with a number of other environmental variables. Fragments of plant debris from the salt marshes that fringe much of Minas Basin commonly occur in the intertidal sediments. It is likely that the deposit-feeders in the area are supported, at least in part, by bacteria within the sediments that degrade this debris.

Previous studies have investigated the relationship of *Macoma balthica* with a variety of environmental parameters, including submergence time (Beanland, 1940; Vassallo, 1969), sediment type (Boyden and Little, 1973), and carbon and nitrogen content of the sediment (Bader, 1957; Newell, 1965; Gilbert, 1969). In this paper, we report the results of an investigation into the relationship between *Macoma balthica* and several environmental factors, including the density of bacteria in intertidal sediments of the Minas Basin.

2. Methods and materials

a. Study area. Samples were collected from the north shore of the Minas Basin, along the stretch of coastline roughly from Economy east to Glenholme (Fig. 1). The intertidal here is up to 2.5 km wide. The grasses *Spartina alterniflora, Spartina patens* and *Puccinellia americana* dominate the marshes. In the intertidal, an upper cobble or sand beach grades downward to muddy sands, in which *Macoma* occurs, along with the gastropod *Nassarius obsoletus*, the amphipod *Corophium volutator*, and various species of the polychaetes *Neanthes* and *Nephthys*. More complete descriptions of the Minas Basin fauna, their distribution and demography are available in Craig (1977) and Yeo (1977).

b. Field methods. Five transects within 37 km were erected perpendicular to the shoreline, and sampled at 50 m intervals during August of 1974. Sample locations are shown on Figure 1. Densities of *Macoma* were estimated by sinking three randomly located cores within a 1 m² quadrat frame located at each station. Total
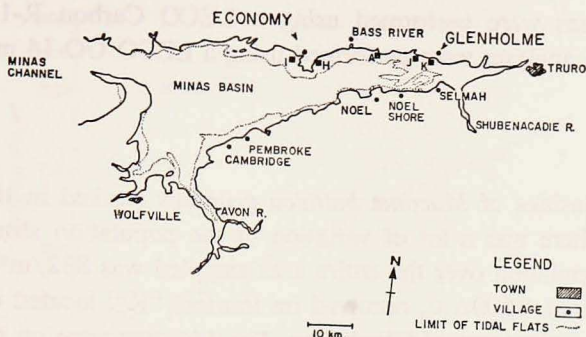
Figure 1. Location of transects.

area of all three cores was 0.06 m². Sediment in the cores was extruded and sieved on the spot, and all *Macoma* enumerated which were greater than 1 mm in length. Excluding areas where *Macoma* were sparse (less than about 100/m²), maximum deviation of core values from the average of all three cores at a station averaged 18%. In high-density areas (greater than about 1000/m²), deviation was about 10%.

Samples for chemical and bacteriological studies were taken, using a sterile spatula to scrape the top 2 to 4 millimeters of mud. These samples were placed in petri dishes, immediately frozen on dry ice, and kept frozen until laboratory analysis.

A separate study investigated the relationship between *Macoma* and grain size of the top 10 cm. of sediment. *Macoma* densities were determined as described above; sediments were analyzed using standard sieve and pipette methods.

c. *Laboratory analysis.* Bacteriological analysis was performed on the samples after they had been frozen at −20°C for four months: Anthony (1963) found no change in bacterial counts of sediments stored six months at −20°C.

Bacteria were enumerated by direct microscopic count, using a fluorescent light technique similar to that described by Dale (1974). Samples were filtered onto 45 mμ Millipore filter paper and stained with a 1:30,000 solution of acridine orange. Filters were dried, cleared with oil, mounted on slides and viewed with a Zeiss fluorescence microscope. Clay particles have a variety of surface and edge charges, and often fluoresce, making distinction of bacteria difficult. Only recognizable coccus and rod bacteria shapes were counted, until 500 bacteria were enumerated for each sample. Filters had to be searched at all levels, due to bacterial penetration. Four successive counts of the same sample differed from each other by less than 10%. Number of bacteria per gram dry weight of sediment was calculated according to Dale's (1974) formula.

Carbon analyses were performed using a LECO Carbon R-12 autoanalyzer. Organic nitrogen analyses were performed using a LECO UO-14 modified nitrogen determinator.

3. Results

Population densities of *Macoma balthica* generally peaked in the middle intertidal, although there was a lot of variation in the population structure with tidal height. Mean population over the entire area sampled was $832/m^2$. The maximum density encountered, $3500/m^2$, occurred on transect "K", located on the extensive flats offshore from the town of Glenholme. The *Macoma* zone on this transect was 500 m wide.

An independent study investigated the relationship between numbers of *Macoma* and sediment grain size. No clams were found in sediments finer than 5.38ϕ (.024mm) or coarser than 2.13ϕ (.23mm). The sediment size appears to set limits to the bivalve's distribution, but within the "allowable" sediment size, no significant correlation was found. Significant correlation ($r = 0.45$; $n = 20$; $p < 0.05$) did, however, exist between density of *Macoma* and the percent weight of sediment less than 4ϕ. Driscoll and Brandon (1973) emphasized the importance of the relative amount of silt and clay in sediments, as a factor in the distribution of the selective deposit-feeder, *Macoma tenta*. ZoBell (1938), Marzolf (1965) and Dale (1974) found higher bacterial numbers in finer sediments. Although a wide variety of sediment grain sizes occurs in the middle intertidal zone of the Minas Basin, there is usually a fine, flocculent surface layer of mud on which *Macoma* may feed.

Organic carbon content of the top few millimeters of sediment ranged from 0.13 to 0.98%, relatively low in view of the high populations of benthic invertebrates, the common occurrence of salt marsh debris on the surface of the sediment, and the development of algal slicks in some areas at low tide. Values of organic nitrogen were very low (0.02-0.05% dry weight of sediment) and because they were at the limit of resolution of the apparatus, precise values could not be determined. C:N ratios ranged from about 6.5 to 19.5, averaging around 11. These samples were taken in late August, the same time of year during which Driscoll (1975) found the greatest values of carbon and nitrogen in Buzzards Bay. Annual variability in the carbon budget for the Minas Basin has yet to be studied.

Bacterial populations ranged from 0.9 to $20 \times 10^9/g$ dry sediment, within the same range as those measured by Anthony (1963), Zhukova and Fedosov (1963) and Dale (1974). Coccus bacteria often occurred within plant stems, supporting the suggestion of Gosselink and Kirby (1974) that bacteria first consume the less refractory internal tissues of plant debris. Bacteria frequently were found attached to sediment grains, although the clustering on the grains recorded by Meadows and Anderson (1966) was not observed, possibly because of the fine grain size of the particles.
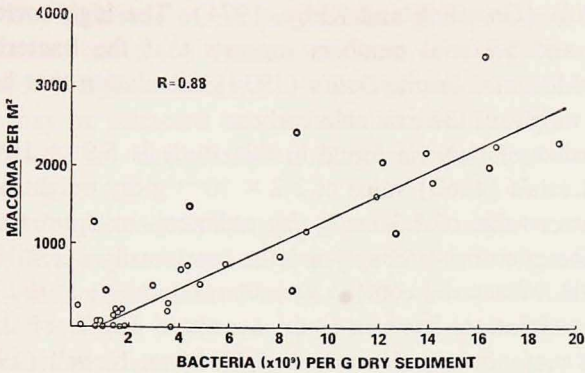
Figure 2. Relationship between population density of *Macoma balthica* and density of bacteria in intertidal sediments.

Results of these analyses are summarized in Table 1. Densities of *Macoma* are positively correlated with densities of bacteria, but not with either tidal height or organic carbon. Multiple regression analysis indicates that densities of *Macoma* may be accurately predicted by bacterial density alone, with 77% of the variance in *Macoma* density values being explained (Fig. 2). Immersion time, as measured by tidal height, is not an accurate predictor of *Macoma* densities.

4. Discussion

Carbon and nitrogen values are very low in this system and high C:N ratios appear to indicate low decomposability of the carbon. Bacterial numbers do not show the correlation with carbon found by Marzolf (1965), Newell (1970) and Dale (1974). The Minas Basin intertidal is characterized by very high tidal currents (which cause the great turbidity in the bay); resuspension of decaying plant material with each tide probably results in transient occurrence of organic matter.

Bacteria represent a basic link in the conversion of low protein refractory detritus to high protein particulate matter that can be cropped by macro-organisms. The conversion efficiency of marsh grass compounds to usable bacterial carbon

Table 1. Correlation coefficient matrix of measured parameters. Sample size = 40.

	Tidal Drop	Macoma Density	Organic Carbon	Bacterial Density
Tidal Drop	1.000	0.247	−0.235	0.181
Macoma density		1.000	0.234	0.880*
Organic carbon			1.000	0.296
Bacterial density				1.000

* significant at $p < 0.01$.

may be up to 66% (Gosselink and Kirby, 1974). The high correlation observed between bivalve and bacterial numbers suggests that the bacteria fulfill dietary requirements for *Macoma,* despite Dale's (1974) calculation that bacterial biomass is only 2.5% by weight of the available carbon.

The mean number of bacteria found in this study is 5.9×10^9 bacteria/g dry sediment. Using Luria's (1960) value of 2.2×10^{-13}g dry weight per cell, bacterial biomass has a mean value of 1.3 mg/g dry sediment, or approximately ⅓ of all carbon present; the microbes probably are the most easily digestible form (ZoBell and Feltham, 1943). Bacterial content varies considerably: at the station with the largest *Macoma* population, bacteria could constitute 100% of the carbon. Bacterial populations may not be independent of *Macoma*. Newell (1965) found that *Macoma* feces increased in nitrogen content as they were populated by microbes, and suggested that *Macoma* reingests the feces to crop the bacteria. A similar "gardening" strategy was investigated by Hylleberg (1975) who found a rich microbial fauna in the feces of two species of *Abarenicola*.

Measured carbon appear too low to support the large *Macoma* populations present. Using the equations of Bubnova (1972), a possible value of the daily carbon requirement of *Macoma balthica* is calculated to be 2.44 mg organic matter. With a conversion factor of 1.8 (Trask, 1955), this value represents 1.35 mg carbon required/day. Both Bubnova and the authors find that a 12-14 mm *Macoma* processes 0.6 g dry sediment per day, and that *Macoma* assimilates 70% of all the organics in the sediment. From Cobequid Bay sediments with average carbon content of 0.40%, *Macoma* may assimilate on the average 1.66 mg organic carbon per day. This amount should be sufficient to satisfy carbon requirements.

A similar treatment for protein by Bubnova, however, gives a daily requirement of 0.78 mg. With his measured protein assimilation efficiency of 62% and a value of 0.05% nitrogen/g dry sediment, the *Macoma* would have to process 5 times the measured rate of sediment to satisfy calculated requirements. These calculations ignore the removal of organics by the other deposit-feeders in the vicinity.

Assuming that Bubnova's equation is correct, it appears that *Macoma* cannot rely solely on deposit-feeding. Possibly the bivalve could increase its rate of feeding but there is doubtless a physiological upper limit. Even given a bacterial multiplication rate of 6 times a day (Hargrave, 1970), there would be insufficient nitrogen present in the sediments. There must be considerable suspension feeding during submergence (suspension feeding has been observed in the field by the authors). Suspended bacteria, detritus and plankton must supplement *Macoma*'s diet. Such a dual life-style has been recognized as a common phenomenon (Stanley, 1970).

The observed distribution of the adult *Macoma* may be determined by larval selectivity. Discrimination of grain size was shown by larvae of the archiannelid *Protodrilus* (Gray, 1966a). An additional attractive factor in the form of a bacterial film was subsequently shown on the chosen sediments (Gray, 1966b) and by

Wilson (1955) for the larvae of the polychaete *Ophelia*. Larval selectivity in the molluscs was demonstrated by gastropod *Nassarius* (Scheltema, 1961). Dale (1974) has shown a high correlation between bacterial numbers and grain size. *Macoma* larvae may be attracted by the bacterial film and thus be indirectly related to sedimentary size characteristics. However, both parameters may be of primary importance.

The high correlation between *Macoma* and bacterial numbers may represent both cause and effect. The mucus-bound fecal pellets of *Macoma* provide an attractive substrate for bacterial colonization: Newell (1965) found a 40-fold increase in the nitrogen content of *Macoma balthica* fecal pellets in 3 days while Hylleberg (1975) observed reingestion of bacterial-rich feces by the polychaete *Abarenicola*. Packaging of the sediment into fecal pellets and pseudofeces decreases threshold pickup velocity and the excreta are then resuspended at high tide (Risk and Moffat, in press). The observed bivalve-bacteria correlation is therefore not a result of a gardening strategy, whereby an individual *Macoma* reingests its own recolonized feces. Most likely the bacteria are attracted by the high fraction of mud and silt. Organic debris and fecal pellets of the flocculent layer are continually resuspended and may not provide a permanent substrate for colonization. Sampling for bacteria was conducted without regard to time of exposure after the water had receded. If bacterial build-up was due entirely to fecal pellet colonization at low tide the time effect would have been evident in the correlation. By packaging its feces, *Macoma* is losing a nitrogen source to the water column.

5. Conclusions

Of the environmental variables elevation, organic carbon and nitrogen, and abundance of bacteria, only the latter was significantly correlated with *Macoma* population densities. Although *Macoma* lives in a variety of sediment types feeding on the fine surface layer of sediment, its densities also appear to be significantly correlated with the amount of fine-grained material in the sediment (in an independent series of samples). When deposit-feeding, *Macoma* utilizes bacteria in the sediments as part of its food requirements. In the sediments examined, bacteria constitute an average of 33% of the total organic carbon, and may in some areas represent 100% of the total.

Calculations show, however, that *Macoma* cannot possibly satisfy its protein requirements by deposit-feeding alone, and hence must suspension-feed when immersed.

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