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Environment Canada

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Field experiments investigating the benthic pelagic coupling over a zebra mussel bed in the Western Basin of Lake Erie

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MANAGEMENT PERSPECTIVE

The foodweb of the Great Lakes Basin on which sport and commercial fish depend may have been altered by the invasion of the bottom feeding Zebra Mussels (Dreissena spp.) They have reached such high population densities that it is feared that their filter feeding will lead to a clarification of the water column and to concomitant removal of food away from pathways leading to important fisheries production. Recent work on marine mussels suggests that physical mixing and related delivery of algal food particles and their utilization by the mussels is of primary importance to understanding their effects on agal populations. Unfortunately, neither the physical mixing in waterbodies like Lake Erie, nor the filter feeding of Zebra Mussels, are well understood.

We conducted biophysical experiments on a mussel infested reef during the summer of 1994 in the Western Basin in Lake Erie. Using current meters and water samples we attempted to characterize the mixing and delivery of algal particles over the reef. In this first reporting of the study we demonstrate by means of a highly simplified model that the filter feeding rates established in the laboratory for Zebra Mussels do not apply in the field. When we compared particle densities upstream and downstream of the reef we could barely detect the effect of mussel feeding. This is important because until now, laboratory results have been extrapolated to the field implying disastrous results. Our analysis is continuing to be refined in order to establish in place feeding rates for the Western Basin.

FIELD EXPERIMENTS INVESTIGATING THE BENTHIC PELAGIC COUPLING OVER A ZEBRA MUSSEL BED IN THE WESTERN BASIN OF LAKE ERIE

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Introduction

Zebra mussels (*Dreissena spp.*) have achieved such high population densities that they have been implicated in the diminution of phytoplankton standing stocks and the clarification of North American lakes (Hebert et al. 1991; Leach, 1993). There has been considerable interest in the ability of these bivalves to filter seston in laboratory and field experiments where clearance rates vary between 2 to 287 ml per mussel per hour (e.g., Kryger and Riisgard 1988; Sprung and Rose 1988 ; Reeders et al. 1989). Much of the recent data obtained in North American laboratories is consistent with these observations, which has lead to the affore-mentioned fear that there will be an alteration of the pelagic ecosystems (cf. Holland, 1993) along with concomitant changes in important fisheries (e.g., Leach, 1993). While there are few data that can bear directly on these issues in freshwater systems (Huttula, 1992), recent work on marine mussels suggests that the physical mixing and related delivery of plankton and its utilization by the mussels is of primary importance to these concerns (Wildish and Kristmanson, 1984; Frechette et al., 1989; Wildish and Kristmanson, 1993). Unfortunately, unlike the relatively-well understood unidirectional tidal flows in coastal marine environments, mixing in freshwater lakes is likely to be primarily wind driven and intermittent (Fischer et al., 1979). Moreover, recent data indicates that flow rate affects zebra mussel filter feeding in a ramp-like manner not predicted by conventional static-flow models (Ackerman, 1994; in review). Both of these outcomes indicate that direct measurements of the physical transport processes and the resultant biology of filter feeding must be made *in situ* to begin to understand the impact of zebra mussels on the pelagic foodwebs. The purpose of the following paper is to report the results of a preliminary study of the biophysical factors that relate to the benthic-pelagic coupling in a zebra mussel bed within the western basin of Lake Erie.

Experimental Procedure

The experimental site was located one kilometer northwest of North Harbour Island in the western basin of Lake Erie as illustrated in figure 1. The site was a shallow reef with a rock and sand bottom. This reef was chosen as the experimental site because it is an isolated bed of zebra mussels completely surrounded by soft muddy sediments. The water depth at the shallowest portion of the reef was 7 m and the average depth of the surrounding waters was 11 m. Visual observations by scuba divers and samples obtained using a mini-Ponar bottom sampler confirmed that there were large numbers of zebra mussels attached to the hard substrate of the reef and negligible numbers off the reef on the soft substrate. From samples gathered by the divers we estimate zebra mussels densities as high as 25,000 per m^2 on the reef.

The outline of the reef and the locations of ten marker buoys are shown in figure 2. The shape of the reef was elliptical with a major axis length of 500 m and a minor axis length of 200 m. The major axis was aligned along a transect from the southwest to northeast. The ten buoys marked the locations of our sampling stations. Four white buoys were located off the reef over the muddy-mussel-free sediments and the remainder were located on the reef. During a five day period (July 11-15, 1994) we conducted an intensive series of attended measurements. Water velocities were measured using an ADCP (Acoustic Doppler Current Profiler) mounted on a small boat in order to determine the streamlines for water sampling. Water samples were gathered along transects following the flow using a second boat. The order and number of stations sampled varied depending on the prevailing winds and currents.

At each station one liter water samples were pumped from five depths. A Turner Designs Model 10-AU Digital Fluorometer was used to measure the fluorescence of each sample. Then the one liter samples were filtered through Whatman Grade GF/C glass microfiber filters for analysis of the seston. The filters were immediately placed in Petri dishes and then wrapped with aluminum foil to prevent degradation of the samples by the ambient light. The samples were stored in ice packed coolers on board the boat and then every evening they were transferred to a freezer.

An array of unattended instruments was moored on the reef from July 6 to August 24. A schematic of the moored instruments showing the geometry of the deployment is shown in figure 3. Four ultrasonic current meters with built-in water temperature sensors, three transmissometers, and a wave and tide recorder were deployed. Meteorological data were obtained from a

Atmospheric Environment Service buoy moored off of Point Pelee (approximately 30 km east of the experiment site). The EG&G model SACM-3 current meters were moored at heights of 0.8 m, 1.1 m , 4.3 m and 5.8 m from the lake bed (note the average water depth at the mooring location was 9.2 m). The current meters were oriented vertically to measure the two horizontal components of the velocity. They were programmed to burst sample the velocity at a rate of 2 Hz for 256 seconds every hour and to record one four minute average of the velocity and temperature every ten minutes. The Sea Tech transmissometers were moored at heights of 0.5 m, 1.2 m and 6.3 m from the lake bed. The Seadata model 365-11 wave and tide recorder was moored on the lake bottom. This instrument senses the water level and wave height using a pressure transducer. It was programmed to record the mean water level once every 10 minutes and burst sample the wave heights at 2 Hz for 256 seconds once every hour. Unfortunately the port of the pressure transducer became partially blocked with sand immediately following deployment. As a result the data for the entire duration of the deployment were corrupted.

Physical Measurements

A plot of the air temperature, wind speed and wind direction is shown in figure 4 for the period of attended measurements, July 11-15. The air temperature ranged from a low of 19 °C at 04:00 GMT (Greenwich Mean Time) on July 11th to a high of 26 °C at 01:00 GMT on July 13th (Note that local time is 4 hours behind GMT). The maximum wind speed (ten minute averages) observed during the week was 11 m/s. The most significant wind event occurred Tuesday morning July 12th. From 23:00 GMT Monday to 08:00 GMT Tuesday the wind changed direction from west to east and increased in velocity from approximately 2 m/s to 11 m/s. This produced wave heights up to 2 m on Tuesday morning and conditions were too rough for the boat equipped with the ADCP and it did not travel to the site that day. The wind speeds briefly peaked again at 11 m/s at 02:00 GMT July 14th but were generally in the range from 5-8 m/s for the remainder of the week.

Water temperature at depths of 3.4 m and 8.4 below the surface are shown plotted in figure 5 for July 11-15. The temperature time series at the upper depth of 3.4 m has a strong diurnal fluctuation due to warming of the surface waters by solar radiation. The temperature increased every day starting at 14:00 GMT (10 A.M. local time) reaching a maximum value at 23:00 GMT (7:00 P.M. local time) and then decreasing as the surface cooled at night. At the lower depth of 8.4 m there is still some evidence of the diurnal fluctuation but it is much weaker. The diurnal fluctuations at the lower depth lag behind those at the upper depth by approximately 2-3 hours. This is an indication of the length of time it takes for mixing processes to transport the warmer surface waters to the bottom. The maximum temperature difference between the two time series is less than 1 °C indicating that there was no significant stratification of the water column.

Water level fluctuations for the time period July 7-20 are shown plotted in figure 6. The time series in the upper plot indicates that the mean water level at the location of the moored wave and tide recorder varied between 9.1 m and 9.5 m over this period. The frequency spectrum is plotted in the lower figure. The first and second modes of wind seiching predicted for Lake Erie have periods of 14.4 hours and 9.1 hours respectively (Hamblin, 1987). There is a peak at approximately 14 hours in the spectrum corresponding to the first mode but there is no evidence of a peak at 9 hours corresponding to the second mode

The average current at heights of 5.8 m and 0.8 m above the lake bed (this corresponds to 3.4 m and 8.4 m from the surface) are plotted in figure 7 for July 11-15. We would expect the current at the lower location to be influenced by the benthic boundary layer. This is confirmed by the data presented in Table 1 where the mean and rms currents at the two heights are compared. Both the mean and rms currents are significantly reduced moving from 5.8 m to 0.8 m above the bed of the lake.

Height	Mean Current	RMS Current
5.8 m	4.1 cm/s	2.4 cm/s
0.8 m	3.0 cm/s	2.0 cm/s

Table 1: Mean and rms current at two heights for July 11-15, 1994.

Two time series of the current sampled in the burst mode at 2 Hz for 256 seconds are plotted in figure 8. The upper plot is the magnitude of the current for 03:00 GMT, July 14 at 0.8 m off the bed. The mean current at this depth is 1.1 cm/s and the rms is 0.41 cm/s. The lower plot is the magnitude of the current for 03:00 GMT, July 14 at 4.3 m off the bed. The mean current at this depth equals 10.65 cm/s and the rms equals 2.5 cm/s. The data in Table 1 shows that the mean current averaged over 5 days at 0.8 m is only reduced by 25% compared to the value at 5.8 m. However, the data in figure 8 shows that there can be much larger differences between the currents at these depths. The mean current is reduced by a factor of 10 and the rms by a factor of 6.

The spectra of the two time series in figure 8 are plotted in figure 9. Note that the vertical scale for the lower plot (5.8 m height) is 10^3 times the vertical scale for the upper plot (0.8 m height). There are two significant spectral peaks in the lower plot at 0.38 Hz and 0.76 Hz. Linear wave theory predicts wavelengths of 11 m and 2.7 m for these frequencies. It would be reasonable to assume that the peak at 0.38 Hz is produced by the orbital motions of wind waves and that the peak at 0.76 Hz is the first harmonic of the nonlinear wind waves. However, the magnitude of the spectral peak at 0.78 Hz is greater than the peak at 0.38 Hz which is not consistent with the assumption that the two spectral peaks are produced by nonlinear surface waves. A Stokes second order wave would produce a spectrum in which the magnitude of the peak at the primary frequency was much larger than the peak at the first harmonic (twice the primary frequency).

Biological Measurements

Samples of zebra mussels were collected from the reef by scuba divers. The size distribution of the mussels was obtained by carefully washing the samples through a set of wire mesh sieves. The mussels were then laid out on sheets of white Mylar and digital images of them were captured using a CCD video camera and frame grabber board. The images were then analyzed using a counting and sizing software package (Global Lab Image) to determine the size distribution. The average size distribution of the mussels is shown plotted in figure 10. The size distribution is bimodal with maxima at 3 mm and 17 mm. The peak at 3 mm represents the mussels recruited in 1994 and the peak at 17 mm represents the 1993 mussels. The specimens collected were all *Dreissena polymorpha*, as no *Dreissena bugensis* were observed (J.D. Ackerman, pers. obs.).

Typical profiles of the total fluorescence and the inorganic and organic concentrations obtained from water samples collected on July 14 are presented in figures 11 and 12. In general both the fluorescence and organic concentration decreases with distance from the surface both on and off the reef, however there was considerable scatter in individual profiles. The inorganic concentration generally increased close to the bed both on and off the reef. In order to reduce the variance of the data we averaged the data over an entire day and compared the profiles of the organic concentration on and off the reef. In figure 13 the average organic concentration profiles on and off the reef are shown plotted. These profiles were obtained by averaging a total of 17 profiles sampled on July 13. Error bars are shown as symbols plotted at plus and minus one standard deviation on either side of the average value at each depth. These error bars indicate that there was significant scatter in the data. If the mussels are having an measurable impact on organic concentrations over the reef we would expect that this impact would be most significant near the bed. Therefore, we compared the mean values at the fourth and fifth depths (lowest two depths) on and off the reef using the Student t test. This statistical analysis is used to determine of the means of two distributions are significantly different. Water samples were collected on a total of four days, July 12-15, therefore there were a total of 8 comparisons made. The results are summarized in table 2.

Date	Degrees of Freedom	t value - fourth depth	t value - fifth depth	critical t - 90% significance level
July 12	10	0.88	0.79	1.81
July 13	17	0.93	1.78	1.74
July 14	16	0.47	3.05	1.75
July 15	8	1.55	0.17	1.86

Table 2: Student t test comparison of the average organic concentrations on and off the reef.

If the values in the third or fourth column are greater than the value in the fifth column then the difference in the means at that depth is significant at the 90% level. The comparison shows that only two depths had significantly different average concentration values on and off the reef, the fifth depth on July 13 and 14. This is somewhat inconclusive but it suggests that the filtering feeding of the mussels has significantly reduced the organic concentrations over the reef.

Steady One-Dimensional Model

The simplest model that can be used to quantitatively estimate the effect of the filter feeding of the mussels on the reef is a steady 1-D model. In figure 14 a schematic of the geometry of the model is illustrated. A bed of zebra mussels is located on the bottom of a lake of constant depth h_o. There is a uniform steady current of U and a uniform organic concentration upstream of the reef of C_o. The density of the mussels on the reef is constant and equal to γ per m^2. The clearance rate of a single mussel equals Q_m m^3/s. If we consider the mass balance of in a slice of water column dx long and a 1 m wide we have,

$$Uh_o\left(C-\frac{\partial C}{\partial x}\frac{dx}{2}\right)=Uh_o\left(C+\frac{\partial C}{\partial x}\frac{dx}{2}\right)+\gamma Q_m C dx \quad (1)$$

where C is the organic concentration which is only a function of x. Equation 1 can be simplified and integrated to give the following solution,

$$C(x)=C_o e^{-\frac{\gamma Q_m}{U h_o}x} \quad (2)$$

where the boundary condition that $C = C_o$ at $x = 0$ has been used. In order to compare model results to our field measurements we need to estimate the clearance rate Q_m, the magnitude of the current U and the density of the mussels γ. Using the bottom samples we estimated that the density of mussels on the reef equaled 25,000 / m^2. However, the samples were collected in locations where the density of mussels was relatively high so it can be viewed as the upper limit of densities on the reef. Ackerman (in review) has measured the clearance rates of zebra mussels as a function of the average water velocity in a laboratory flume. He found that the clearance rate is a strongly dependent on the velocity of the flow over the range 0 - 20 cm/s

Equation 2 is shown plotted in figure 15 for the case when $h_o = 10$ m, $U = 5$ cm/s, Q_m = 90 ml/hour and $\gamma = 1000$, 5000, 15000 and 25000 mussels/m^2. The model predicts that with 25,000 mussels/m^2 that the concentration will be reduced by 22% if the bed of mussels is 200 m long. With 5000 mussels/m^2 the initial concentration is reduced by 5% in 200 m. This model is obviously very crude because it assumes that the benthic-filter-feeding mussels have access to the entire water column. That is, the water column is assumed to be completely mixed at all times. In figure 16, model predictions from eq. 2 with $h_o = 10$ m, $\gamma = 5000$ mussels/m^2, U = 1, 5, 12 and 19 cm/s and clearance rate values from Ackerman (in review) are shown plotted. As expected the model predicts that the mussels are more effective at reducing the concentration at the lower velocities. This is because the water takes longer to advect along the reef and therefore the mussels have more time to remove algae from a particular volume of water.

At our experimental site the average depth over the reef is approximately 8.0 m and the depth of the surrounding waters 11.0 m. We assume that the reef does not present a significant obstacle to the flow i.e. water flows over the reef as opposed to being diverted around it. Therefore,

$$(Uh)_{off} = (Uh)_{on} \tag{3}$$

where U is the mean velocity and h is the depth. If this is true and there are no mussels on the reef or the impact of the mussels is negligible then the flux of organic material will also be equal,

$$(UhC)_{off} = (UhC)_{on}. \tag{4}$$

We conclude then that if the impact of the mussel filter feeding is negligible and the algae can be treated as a conservative tracer then $C_{off} = C_{on}$. The plots of the average organic concentration profiles in figure 13 and the t test results in table 2 showed that the concentrations on and off the reef were not significantly different. The exceptions to this were the concentration next to the bed on July 13 and 14 which were significantly different at the 90% level.

The model predicts dramatic reductions in the concentrations over a mussel bed while the field observations show that there is only very small reductions in the organic concentrations over the reef. The only reasonable explanation for this is that the zebra mussels are much less efficient at filtering algae from the water than the model assumes. The mussels are benthic filter feeders and therefore must rely on physical processes to deliver food to them. As a result the properties of the flow above the mussel bed can have a profound impact on the food supplied to the mussels. It is unlikely that the water column is completely mixed on the time scale it takes for water to advect across the reef. The mussels are submerged in the benthic boundary layer and the turbulent diffusion that transports fluid and hence nutrients vertically in the water column is suppressed and in fact approaches zero at the lake bed. It appears that the ability of zebra mussels to remove algae from the water is limited not by their capacity to filter water but by the rate at which the ambient flow delivers algae to the mussel bed.

Conclusions

Although work is in progress our preliminary results suggest a complex flow field over the zebra mussel bed. The current field is composed of longer term fluctuations related to lake seiching and direct wind forcing which at any instant in time can lead to a flow which varies significantly in direction and magnitude from one depth to another. Superimposed on this longer term variation are highly variable currents associated with wave orbital motion and which are of the same order of magnitude as the longer term flows. Finally, the mussels must contend with even higher turbulent velocity fluctuations which are not resolved by our instrumentation.

By means of a simple model we have demonstrated that the extrapolation of individual laboratory-based feeding rates to a field situation leads to a significant overestimation of the actual feeding rates. There are several possible reasons for this overestimation, namely, the interaction between mussels when they occur in dense concentrations reduces their clearing efficiency and the development of a low concentration layer near the bed which is not accounted for in our simple model. Further work is in progress to refine the model to allow for vertical variability in organic concentration, a more accurate prescription of the turbulent transport of organic material above the bed and to validate other model assumptions such as the assumption of two-dimensional flow over the bed.

Acknowledgments
The authors are grateful to the Great Lakes University Research Fund and the University of Toronto for providing the funds for this study. We would also like to thank M.Charlton for his helpful comments during the preparation of this paper.

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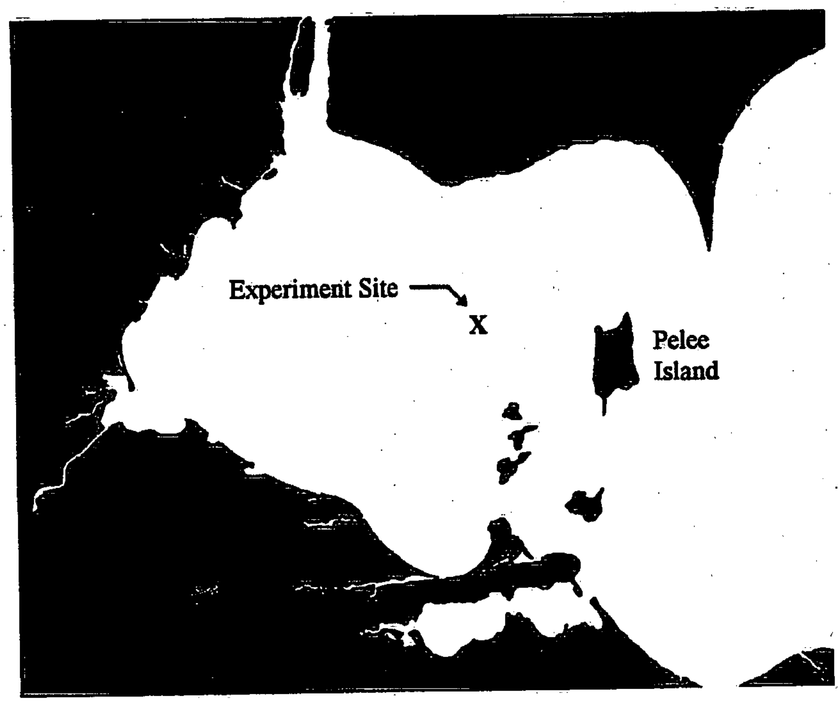


Figure 1: Map of the western basin of Lake Erie showing the location of the experiment.

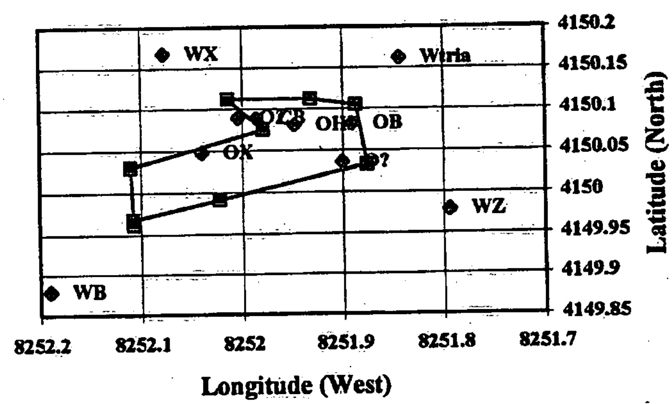


Figure 2: Map showing the location of the sampling stations. The square symbols connected by the solid line show the locations where zebra mussels were collected using a mini-Ponar bottom sampler. Therefore the enclosed area is a very crude outline of the reef.

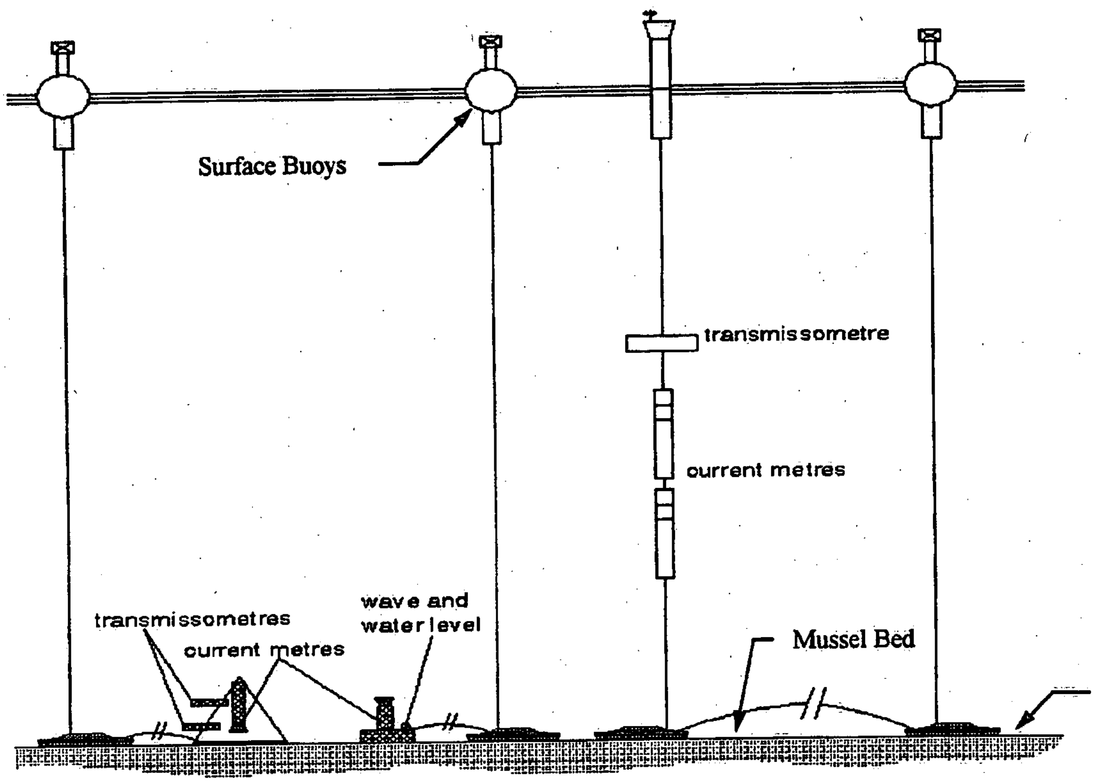


Figure 3: Schematic of the moored instruments.

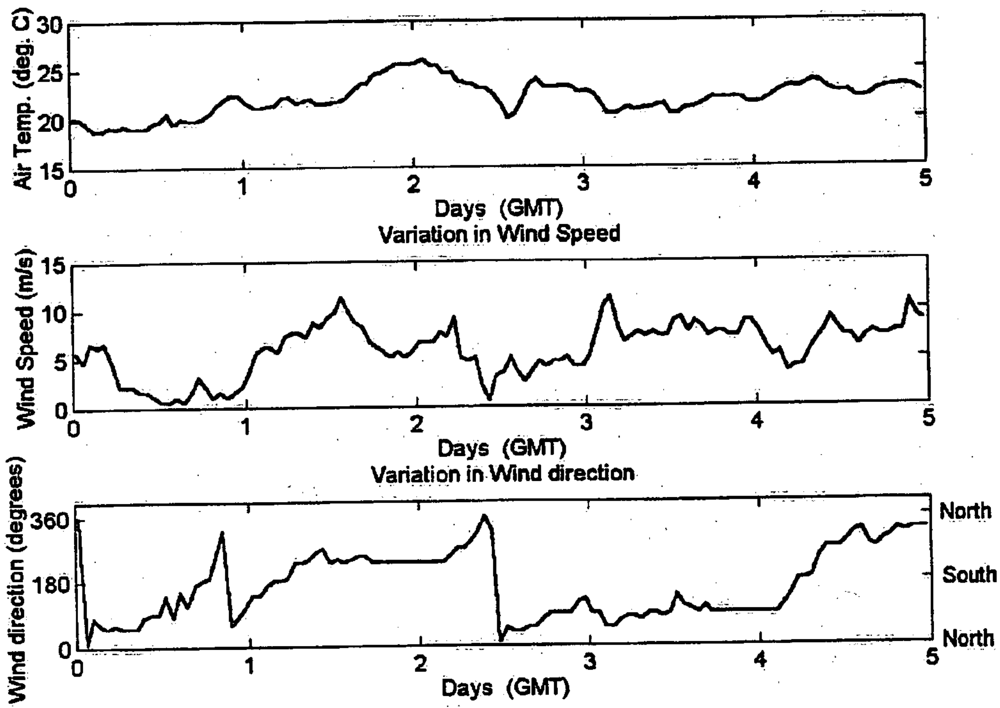


Figure 4: Air temperature, wind speed and wind direction for July 11-15, 1994.

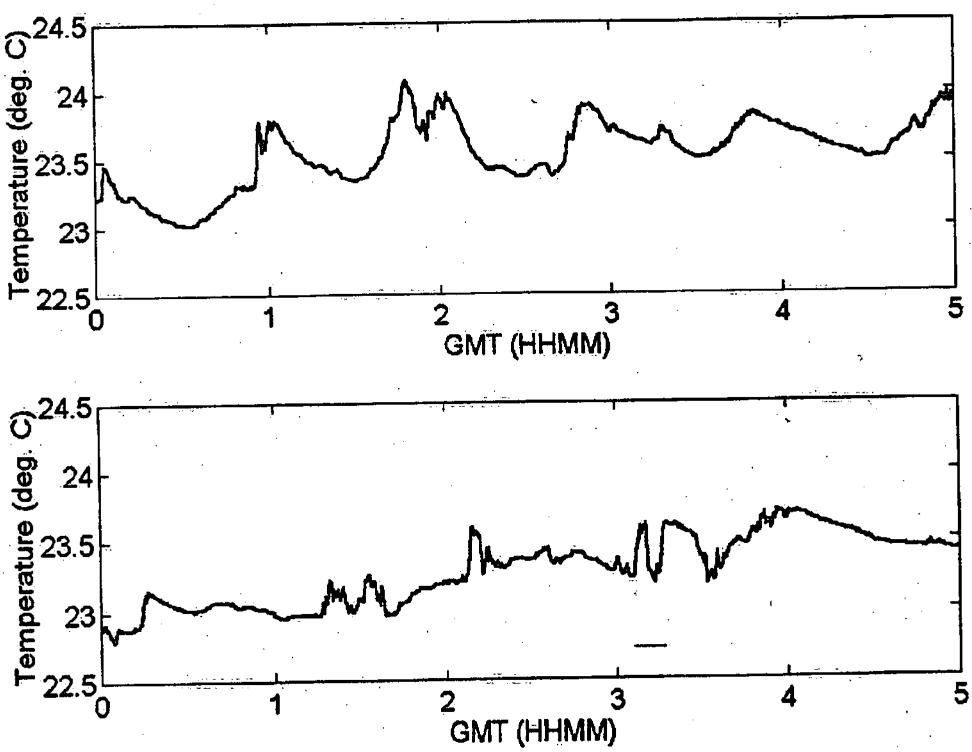


Figure 5: Water temperature at 3.4 m and 8.4 m below the lake surface for July 11-15, 1994.

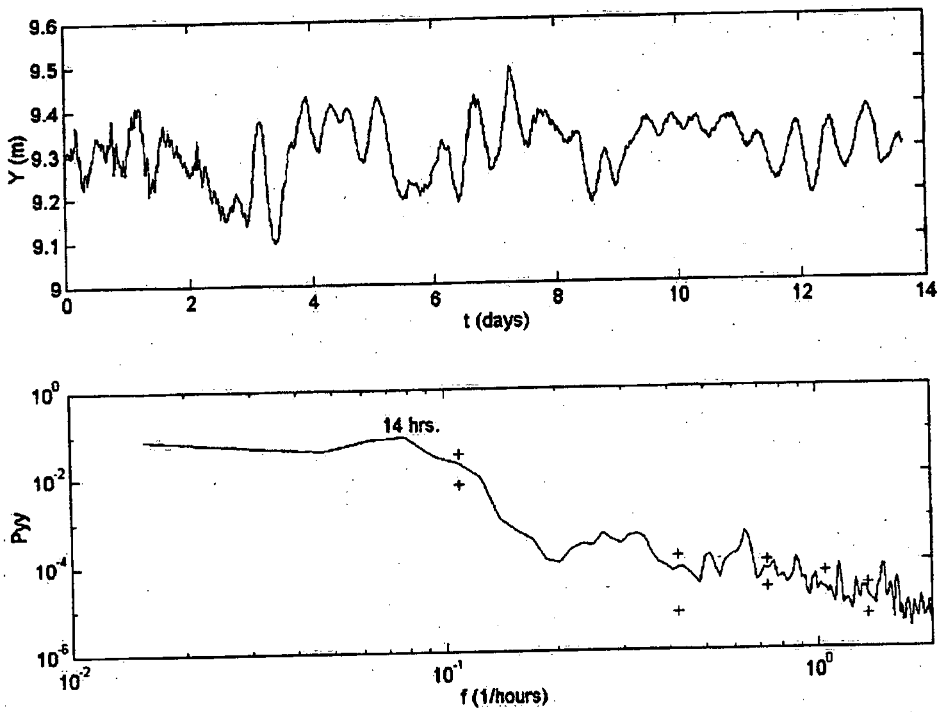
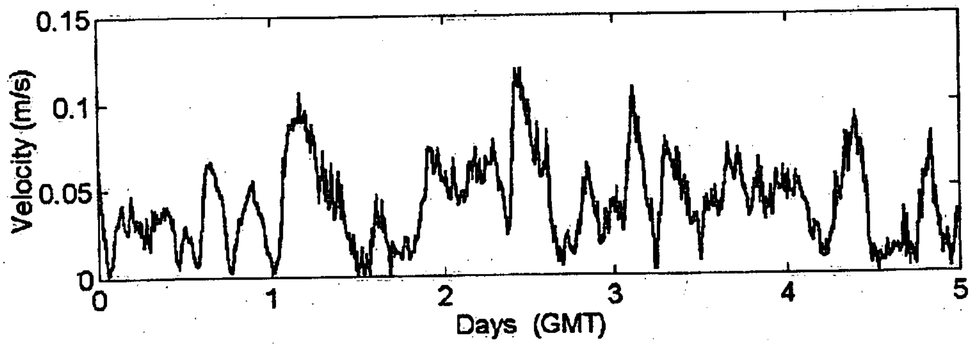


Figure 6: Upper plot is a time series of the water level from July 7-20, 1994. The time series is 1372 points sampled every 15 minutes. The lower plot is the frequency spectrum of the water level computed by computing using 256 point segments, overlapping 128 points and applying a 256 point Blackman window. The + symbols indicate the 95% confidence interval of the spectrum.



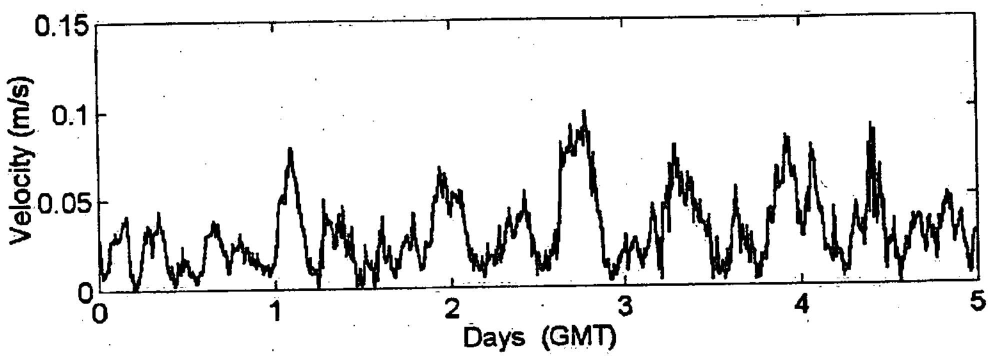


Figure 7: The average current at heights of 5.8 m (upper plot) and 0.8 m (lower plot) above the lake bed for July 11-15, 1994. The average current is obtained by sampling every ten minutes at a rate of 2 Hz for a period of 4 minutes i.e. averaging 480 points.

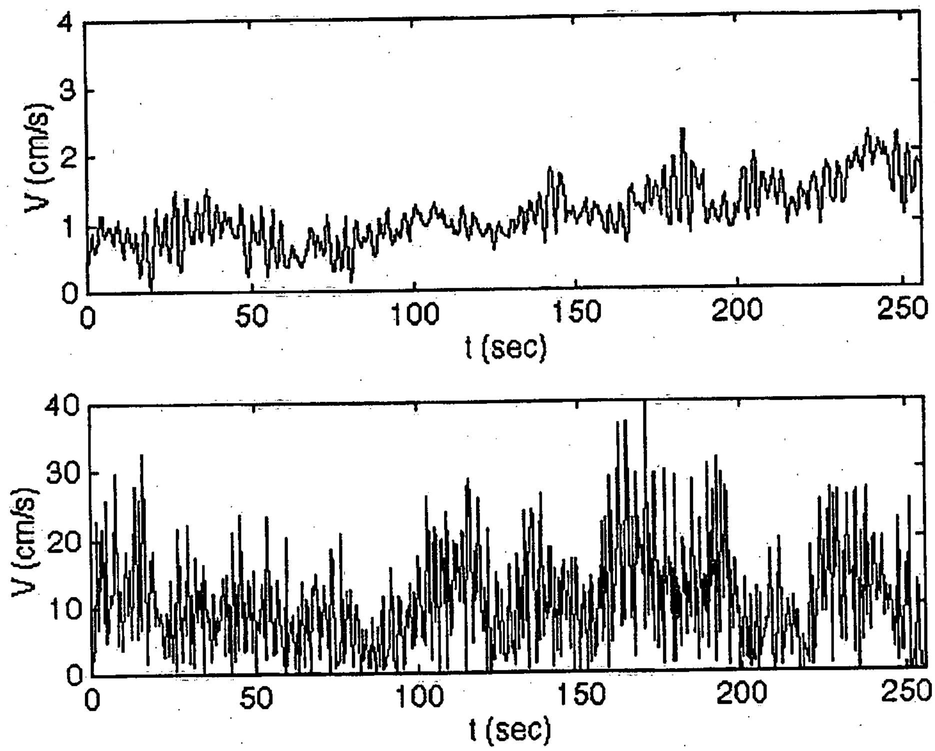


Figure 8: Two time series of the current sampled in the burst mode at 2 Hz for 256 seconds for 03:00 GMT, July 14, 1994. The upper plot is the magnitude of the current at 0.8 m above the bed and the lower plot is the magnitude of the current at 4.3 m above the bed

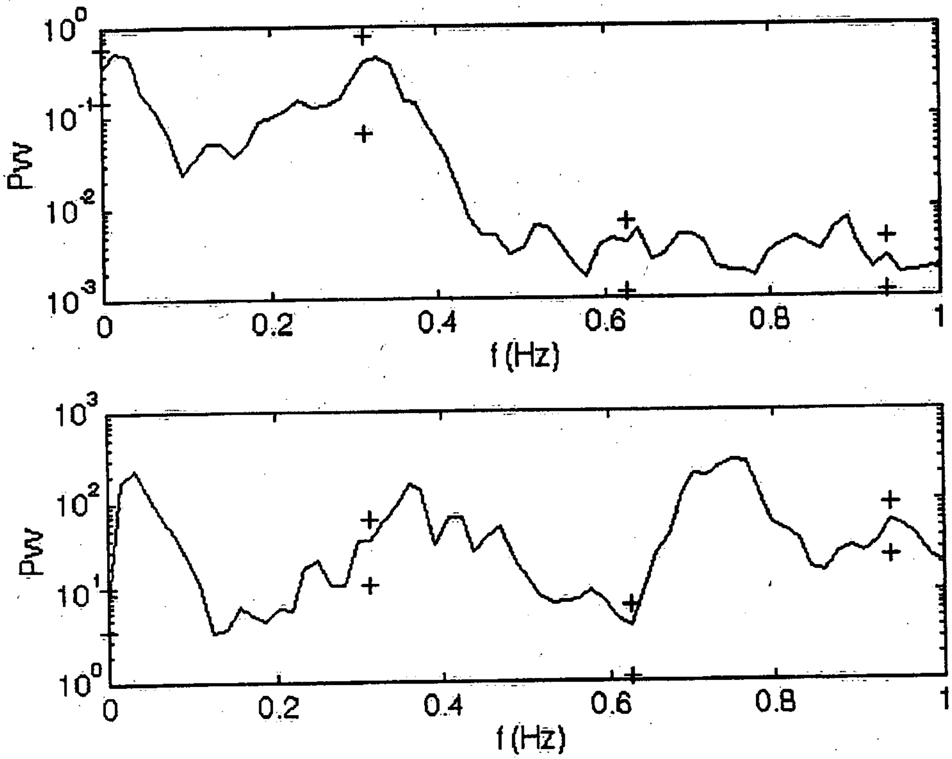


Figure 9: Frequency spectra of the burst current meter time series in figure 8. The upper plot is the spectrum corresponding to 0.8 m above the bed and the lower plot 4.3 m. The spectra were compute from the 512 point times series using 128 point segments, 64 point overlap and a 128 point Hanning window. The + symbols are the 95% confidence limits of the spectra.

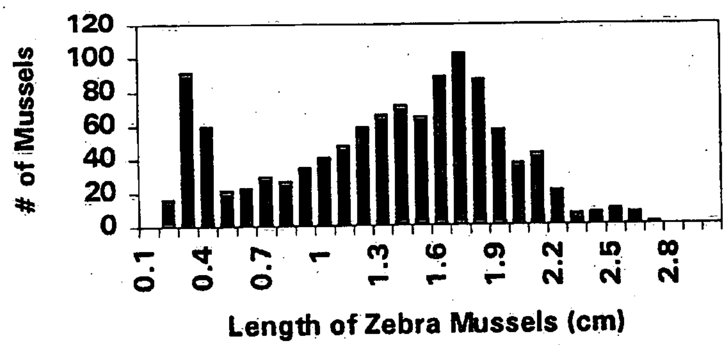


Figure 10: Mussel size distribution obtained from three grab samples collected by scuba divers.

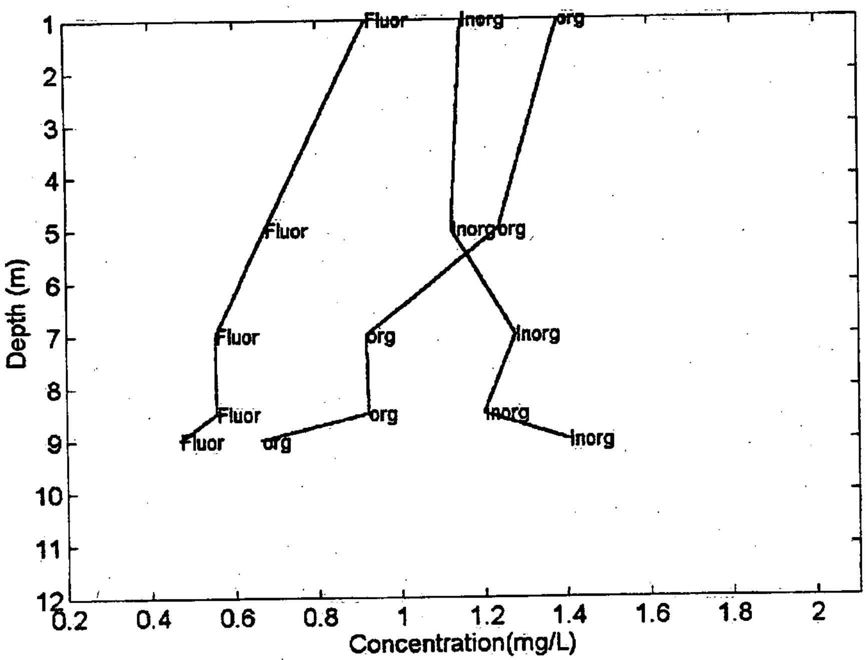


Figure 11: Typical fluorescence (Fluor) in arbitrary units, organic concentration (org - mg/liter) and inorganic concentration (Inorg - mg/liter) over the reef on July 14, 1994.

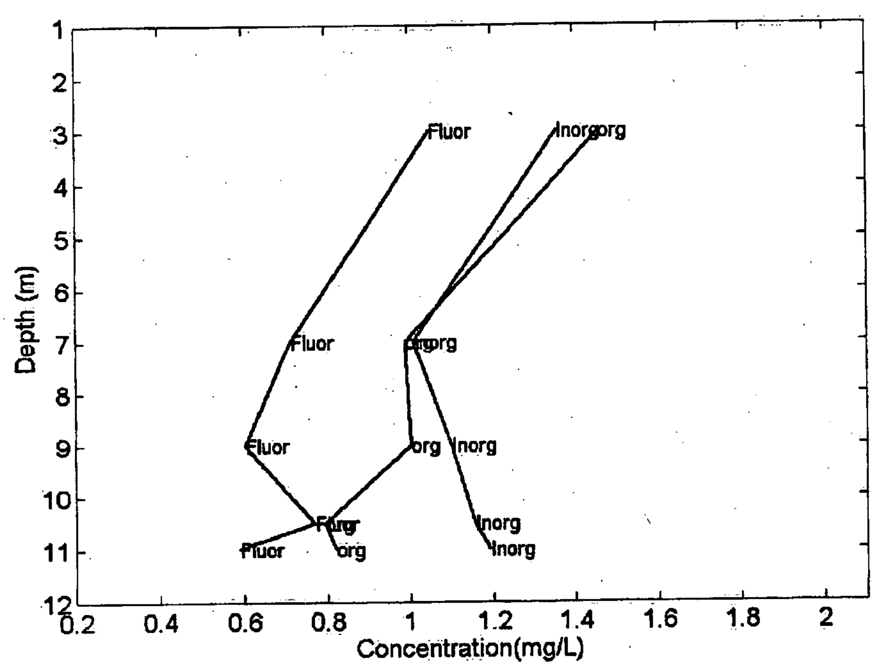


Figure 12: Typical fluorescence (Fluor) in arbitrary units, organic concentration (org - mg/liter) and inorganic concentration (Inorg - mg/liter) off the reef on July 14, 1994.

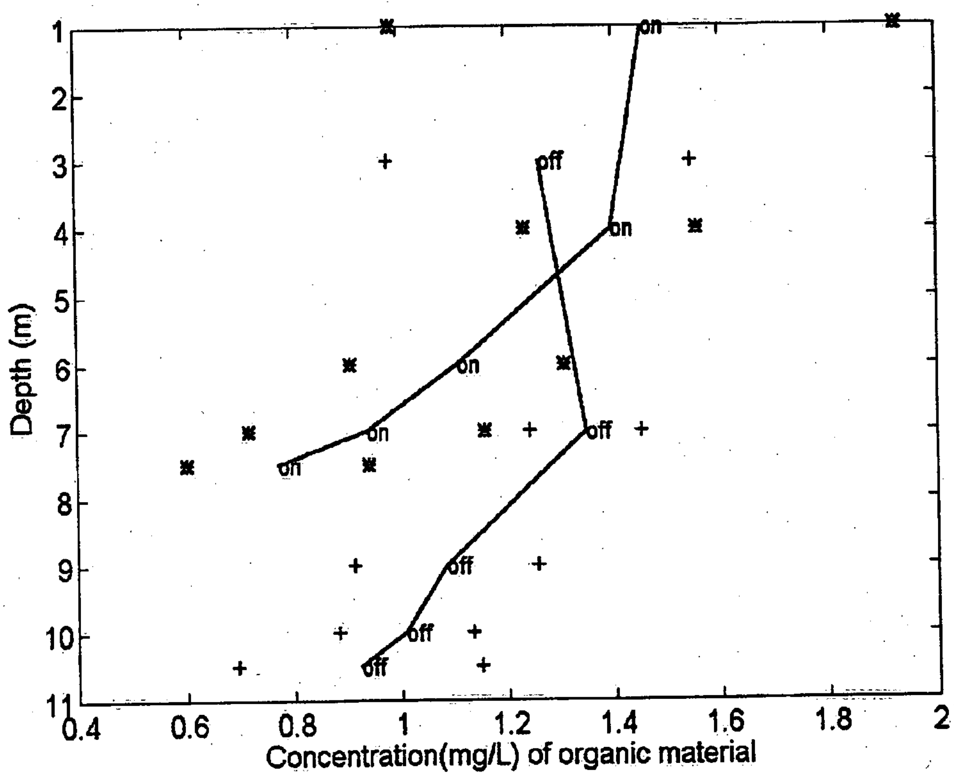


Figure 13: Average organic concentration profiles on and off the reef for July 13, 1994. The + and * symbols are plotted ± one standard deviation from the average values.

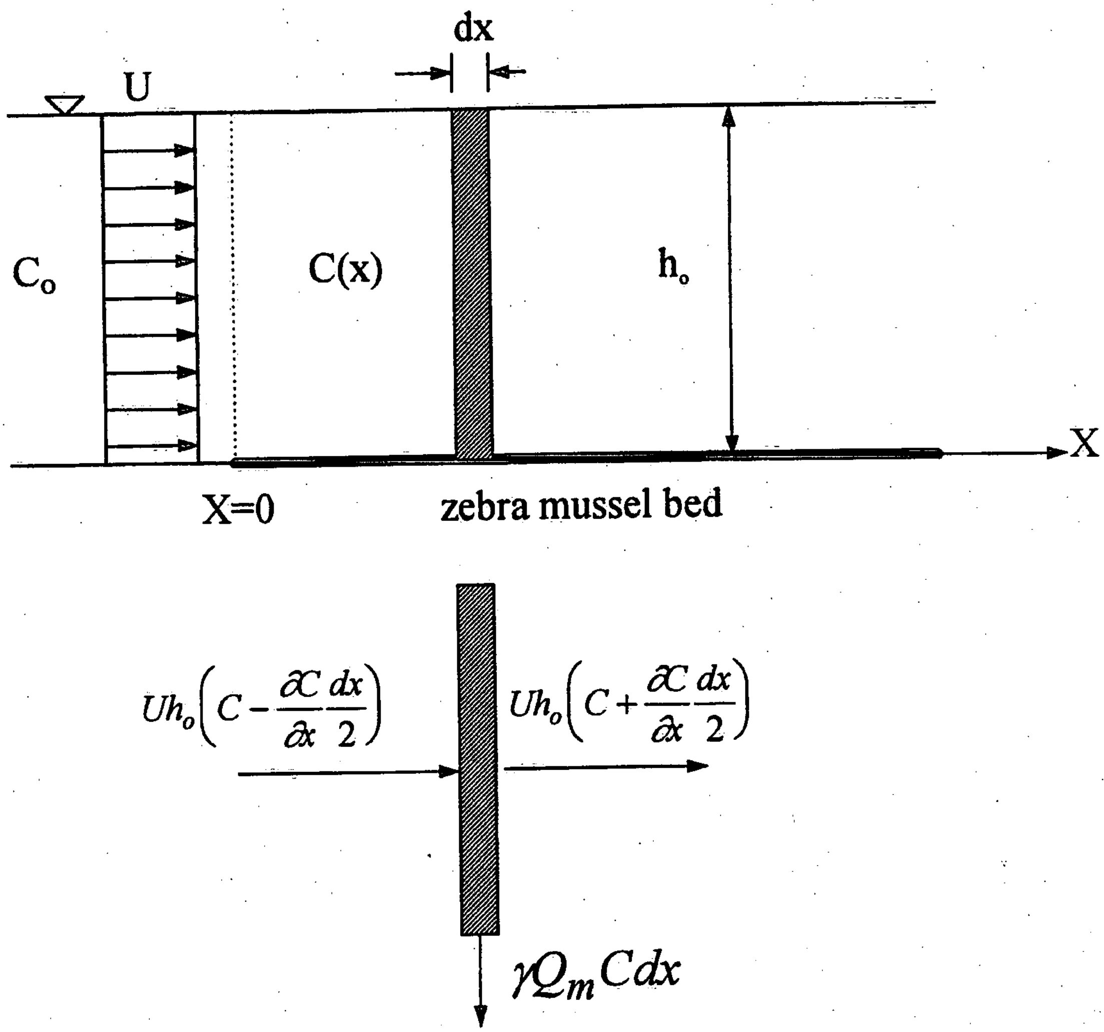


Figure 14: Schematic of the geometry for the model.

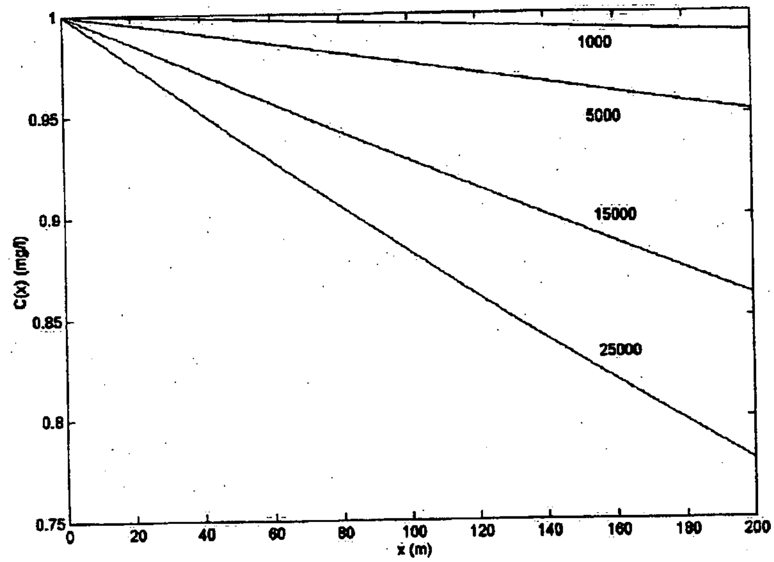


Figure 15: Model predictions (eq. 2) for the concentration C(x) as a function of distance x from the leading edge of the mussel bed. Equation 2 was evaluated with $h_o = 10$ m, $U = 5$ cm/s, $Q_m = 90$ ml/hour and $\gamma = 1000$, 5000, 15000 and 25000 mussels /m^2 .

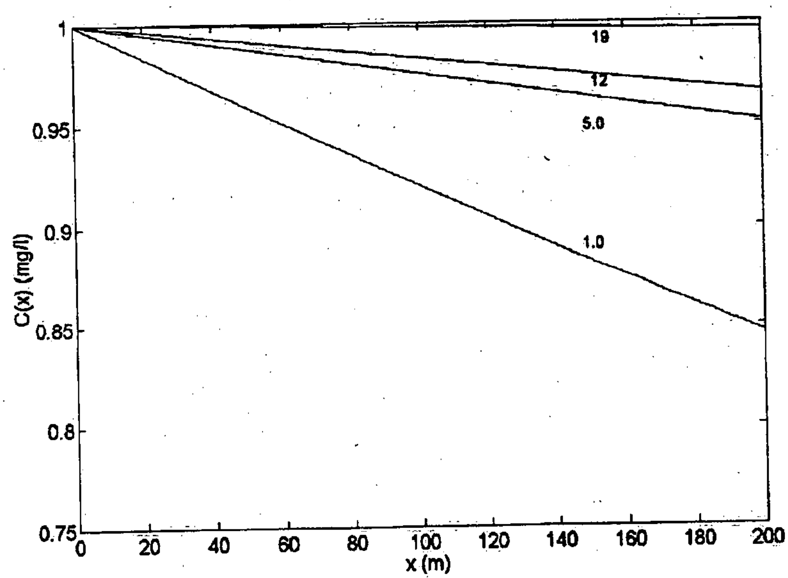


Figure 16: Model predictions (eq. 2) for the concentration C(x) as a function of distance x from the leading edge of the mussel bed. Equation 2 was evaluated with $h_o = 10$ m, $\gamma = 5000$ mussels /m^2 and U = 1, 5, 12 and 19 cm/s. Note the clearance rates at the four velocities are taken from Ackerman (in review).

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