Vol. 114: 117-127, 1994

MARINE ECOLOGY PROGRESS SERIES
Mar. Ecol. Prog. Ser.

Published November 3

Seston variability and daily growth in *Mercenaria mercenaria* on an intertidal sandflat

Michael J. Bock, Douglas C. Miller

Graduate College of Marine Studies, University of Delaware, Lewes, Delaware 19958-1298, USA

ABSTRACT: We conducted observations of weather and water column parameters to determine the scope and persistence of seston variability on an intertidal sandflat (Cape Henlopen, Delaware, USA) and the effects of this variability on the daily growth rate of the hard clam *Mercenaria mercenaria*. Wave-induced resuspension of bottom sediments was found to increase the quantity of particulate matter in the water column by an order of magnitude. At high suspended loads, the quality of the seston, measured as the percent organic matter, was reduced by a factor of 5 due to the dilution of the organic matter with inorganic particles. The seston parameters (suspended solids, particulate organic matter and percent organic) responded quickly to changes in the weather, showing no significant autocorrelations at lags greater than 1 or 2 d. Daily shell growth increments of *M. mercenaria* were measured using shell microgrowth techniques. The daily growth rate was compared to the seston parameters and the water temperature. For 2 independent implantations, the daily mean ensemble and individual clam shell growth increments were significantly correlated to the quality of the seston. The composition of the seston was demonstrated to be more important to clam growth than the concentration alone. Shell growth responded to changes in the percent organic matter on a daily time scale, with no lag or memory to previous seston parameters. These results provide direct, field evidence for the influence of particle quality on clam growth on a daily time scale.

KEY WORDS: Environmental variability · Bivalve growth · Seston · Intertidal sandflat

INTRODUCTION

To date, there is a large body of evidence supporting the contention that particle transport and fluid flow are intimately linked to the feeding behavior and growth of shallow water benthos (e.g. Nowell & Jumars 1984, Muschenheim 1987, Monismith et al. 1990, Turner 1990, Levinton 1991, Turner & Miller 1991a, b, Miller et al. 1992). For example, the growth of suspension-feeding bivalves is coupled to conditions in the water column, from which they derive their nutrition (e.g. Bricelj et al. 1984, Peterson et al. 1984, Peterson & Black 1987, Fréchette et al. 1989, Grizzle & Lutz 1989, Grant et al. 1990, Turner & Miller 1991b). However, the magnitude and time scale of the effect on the growth response are largely unknown. To determine the range of relevant conditions in the water column and the effects of these changes on the organisms, it is imperative to simultaneously measure environmental variability and its effects on the benthos.

Only a few studies have looked at the extent of environmental variability affecting the near-shore benthic environment in the field, either on long (Emerson & Grant 1991) or short time scales (Miller & Sternberg 1988, Fegley et al. 1992). These studies have shown that field conditions can vary greatly over time scales ranging from seconds to years. Storms provide one mechanism for roughly daily environmental variability (Miller & Sternberg 1988). One of the most dramatic storm-induced changes is an increase in the wind stress. Since surface gravity waves are predominantly wind driven, an increase in wind stress would serve to increase wave height and thus affect the near-bottom flow regime. Higher waves often lead to an increase in sediment transport and suspension (e.g. Miller & Sternberg 1988, Zampol & Inman 1989).

Sediment supply, fluid flow and particle flux affect the feeding rate and feeding mode of many benthic species (e.g. Jumars & Self 1986, Miller & Jumars 1986, Levinton 1991, Miller et al. 1992). Increases in suspended matter have been found to either increase (e.g. Rhoads et al. 1984, Bayne et al. 1987, Grant et al. 1990) or decrease (Bricelj & Malouf 1984, Bricelj et al. 1984, Grizzle & Lutz 1989) the feeding and growth rate of suspension-feeding bivalves. For *Mercenaria mercenaria*, the growth rate can be reduced during periods of high suspended sediment concentrations (Turner & Miller 1991b) and storm events (Kennish 1980).

In this study, we quantified daily environmental variability on an intertidal sandflat over 4 lunar months. These results characterize the scope and persistence of environmental variability, specifically the implications of the change from quiescent conditions to more energetic conditions. We explored the relationship of this variability to the growth of the hard clam *Mercenaria mercenaria* by measuring daily shell growth increments and correlating them with the measured environmental parameters. We used these results to determine which water column parameters most influenced clam growth at the study site.

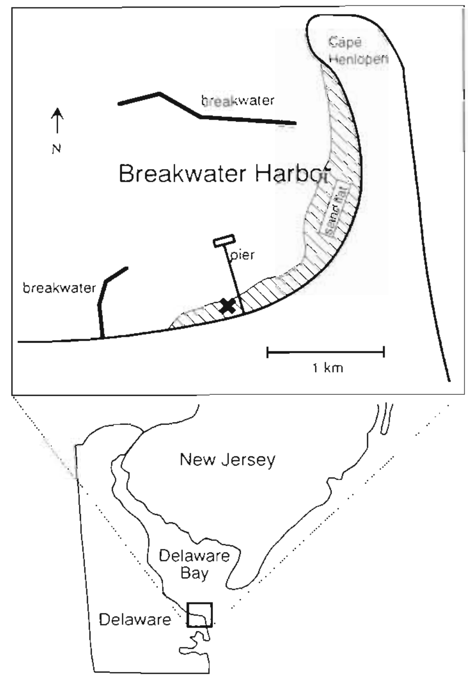

Fig. 1. Breakwater Harbor, Delaware, USA. The sand spit of Cape Henlopen is to the east. Breakwaters have been constructed to the north and to the west. The hatched area is the intertidal sandflat. The study site (**x**) is located just west of the fishing pier

MATERIALS AND METHODS

Our goal was to characterize the effects of environmental variability on the near-shore environment by performing daily measurements of wind, waves, seston and shell growth of *Mercenaria mercenaria*.

Study site. The experiments were performed on the intertidal sandflat at Cape Henlopen (Delaware, USA), which is located at the junction of Delaware Bay and the Atlantic Ocean (38° 46' N, 75° 06' W). The sandflat is within the confines of Breakwater Harbor, with limited exposure to Delaware Bay (Fig. 1). It is protected by the large sand spit of Cape Henlopen to the east and breakwaters to the north and west. The tides are semi-diurnal, with a mean tidal range of about 1.3 m (Polis & Kuferman 1973). The sediment is a well-sorted, medium sand (Ray 1989) and is populated by numerous polychaetes, hemichordates, mollusks, crustaceans, benthic diatoms and meiofauna (Kinner & Maurer 1978, Miller et al. 1992, authors' pers. obs.).

Environmental parameters. Over 4 lunar months, we quantified environmental variability in Breakwater Harbor Daily measurements were performed during daylight low tides between 23 August and 18 December 1991, missing only 11 d over a 118 d sampling period. Measurements included: wave height, wave period, wind speed, wind direction, air temperature, water temperature, suspended solids and the particulate organic matter (POM) of the suspended solids.

We measured wind parameters with a hand-held anemometer. The wind speed was the highest value sustained for at least 5 s. Since Breakwater Harbor is open to the Delaware Bay to the north-northwest, waves entering the harbor through this passage should have the greatest influence on waves (see Fig. 1). To account for this effect, the wind speeds were multiplied by the cosine of the deviation of the wind direction from the NNW entrance to the harbor. If the wind direction was greater than 90° from NNW, the corrected wind speed was set to zero. We measured water temperatures using a thermocouple (±0.1 °C) and salinity using a standard conversion of the output from a conductivity meter (±0.1 ppt). Wave data were the average period and height of 10 consecutive waves, measured visually in water 30 cm deep in wave troughs. To quantify the suspended material, three 1 l water samples were collected by submerging bottles just below the water's surface. From each sample, 300 ml was filtered through pre-weighed, glass fiber filters (Whatman GF/A, 1.6 µm nominal pore size), and rinsed twice with 100 ml of deionized water to remove salts. Filters were dried overnight at 60°C and weighed to determine the suspended solids concentration. Dried filters were ashed overnight in a muffle furnace at 450 °C (Williams 1985) and the POM in the water column was measured as the mass loss on ignition (Hirota & Szyper 1975). We expressed the ratio of the POM to the total suspended solids, multiplied by 100%, as the percent organic matter of the seston.

Hard clam growth rate. We explored the relationship between the growth rate of *Mercenaria mercenaria* and the parameters described above. We used juvenile clams to avoid the problems in correlating shell growth to tissue growth in reproductively active bivalves (Kautsky 1982). Mercenaria Manufacturing (Millsboro, DE) provided yearling clams of about 20 mm in length. In each of 3 consecutive intervals, 30 clams were deployed in a 1 m^2 mesh enclosure on the sand flat. The mesh extended about 15 cm below the sediment surface, 1 cm above the surface and remained uncovered. Peterson et al. (1983) and Turner (1990) have successfully used similar enclosures. Before being placed in the enclosures, the shells were numbered with a dental bit, and weighed and measured with digital calipers. The clams were then placed in a refrigerator overnight at 4 °C to induce a stress line in the shell microstructure as an indicator of the beginning of each implantation. We deployed the first group on 30 July 1991 and recovered them on 25 September 1991, for a total of 57 d. It is important to note that although the first group was implanted 30 July, environmental data was collected beginning 23 August, thus limiting this group's growth time series to the latter 34 d. During the interim period we performed preliminary work to develop our daily sampling protocol. The second group was in place for 63 d from 25 September 1991 to 27 November 1991, and the third group for 56 days from 27 November 1991 to 22 January 1992. Following recovery, the clams were measured again, and we performed microgrowth analysis to determine daily growth increments.

We used the techniques described by Rhoads & Pannella (1970) and Kennish (1980) to measure the daily shell growth increments. For the first 2 implantations, all recovered clams were analyzed for microgrowth, for a total of 16 clams in the first group and 15 in the second. There was almost no new growth in the third group and so microgrowth analysis was not attempted. For the analyzed clams, the tissue was separated from the shells, and 1 valve was embedded in an epoxy resin. The shells were cross-sectioned along the axis of maximum growth with a low-speed diamond saw. Polished, planar cross-sections were etched with 1 % HCl for 30 s to expose the daily growth lines. The cross-sections were wetted with acetone, and an acetate sheet was placed on top. When the acetate was dry, an impression of the growth lines in the shell remained. We classified lines which extended from the outer (prismatic) layer into the inner (homogeneous) layer (Pannella & MacClintock 1968) as daily growth lines. These growth lines were viewed with a compound microscope, and distances were measured using an image analysis system (Cue-2 image analysis system, Olympus Corp., Cherry Hill, NJ, USA). Typical increments were between 40 and 100 µm, with a measurement error of <5 µm. Growth increments were easy to resolve using this technique and the clams were found to have microgrowth increments equal in number to the days implanted based on the temperature stress line induced at the beginning of the implantation. Previous work with clams from the same stock also found that the growth lines have a daily periodicity in Rehoboth Bay, a nearby coastal lagoon system, and in laboratory reared clams (Appendix A in Turner 1990).

Data analysis. Data were analyzed using the SYSTAT statistical package (Wilkinson 1990). Results are presented graphically using time series and quantile plots. For the quantile plots, values are plotted versus their cumulative proportion of the data. Cumulative proportion represents that fraction of the observations less than or equal to the corresponding value on the abscissa. For example, 0.5 represents the median and 0.75 represents the upper quartile: 75% of the data are smaller and 25% are larger than the value. A symmetrically distributed data set will plot in an 'S'-shape. For statistical tests, the conventional critical α-level of 0.05 was used to assess statistical significance. When appropriate, Bonferroni's adjusted probabilities were used to protect against unwarranted inferences of significance in multiple comparisons (Miller 1981). If a Bonferroni adjusted p was greater than 1.0, a value of 1.0 was reported. For the autocorrelations and the cross-correlations (Chatfield 1984), SYSTAT interpolates between missing values using distance-weighted least squares (Wilkinson 1990).

RESULTS

We collected daily environmental data over 118 d. Caliper shell growth parameters were measured in 3 independent implantation periods, and we performed shell microgrowth analysis on the first and second implant groups.

Time series results

A total of 107 daily measurements was performed over 118 d. The salinity at the study site averaged 28 ppt and ranged from 26 to 30 ppt. Time series plots of air temperature, water temperature, tidal range (from NOAA tide tables), cosine-corrected wind speed, suspended solids and the POM are shown in Fig. 2. There is a general, seasonal trend of decreasing temperature with time. The cosine-corrected wind speed plot shows that there are periods of calm winds punctuated by periods of greater wind speed, usually coinciding with the passage of frontal storms. Given the

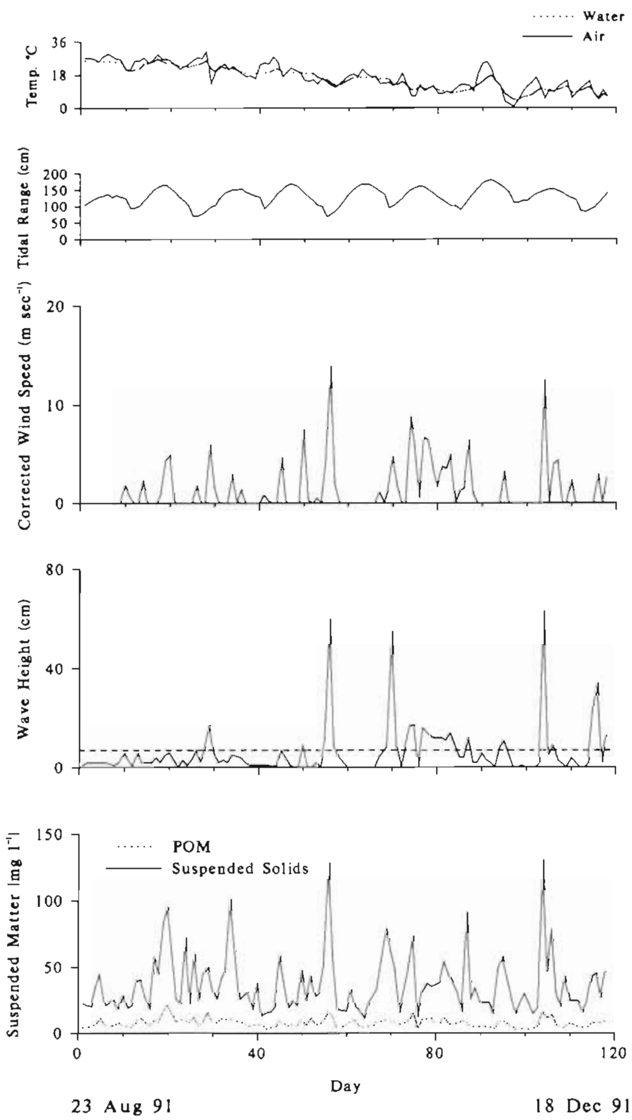

Fig. 2. Time series plots of the daily environmental data. The dotted line at 7 cm in the wave height time series represents waves estimated to move the medium sand of the sandflat

exposure and geometry of Breakwater Harbor, the wave height data closely follows the cosine-corrected wind speed, as expected. The dotted line in the wave height plot represents waves of 7 cm in height. Linear wave theory calculations (e.g. Dean & Dalrymple 1984) show that waves of this height or greater can transport the bulk sediment in 50 cm of water depth (e.g. Sleath 1984, Miller et al. 1992), and 7 cm was used as a threshold for storm conditions

Quantile plots were used to examine the distribution of the measured parameters (Fig. 3). The quantile plot of wave heights shows that about 25% of the time waves were 7 cm or greater. It also shows that the values are skewed, with high values being less frequent. The suspended solids values are also asymmetrical, with a small number of high values that are generally associated with storm waves (≥7 cm in height, plotted as diamonds in Fig. 3). The POM data show the same pattern. The percent organic quantile plot is 'S'-shaped, indicating a more symmetrical distribution, with the values associated with storm waves tending to be lower.

Many of the measured parameters could be interrelated due to cause and effect or similar responses to a forcing process. These relationships can be explored by examining the Pearson's correlation coefficients and Bonferroni's adjusted probabilities found in Table 1. The wave height was significantly correlated to all of the measured water column parameters. This relationship is also shown in Fig. 4. Large waves increased the suspended solids and POM and decreased the percent organic, again implicating dilution of the organic matter. The percent organic was significantly and negatively correlated with the suspended solids, but it was not correlated with the POM (Table 1).

The parameters described above also may be linked in time, i.e. the conditions on one day may affect the conditions on the next day. We used autocorrelation (Chatfield 1984) to determine the temporal dependency of a parameter on previous values. Autocorrelation plots of the cosine-corrected wind speed and the water column parameters can be found in Fig. 5. The plot of the corrected wind speed shows that there was a significant correlation between wind speeds obtained on consecutive days. The suspended solids were also autocorrelated at a lag of 1 d. The POM was correlated at lags of 1 and 2 d. There was no autocorrelation in the percent organic data, implying that there was little temporal dependence in these values.

Cross-correlation plots (Chatfield 1984) were used to determine if there was any time dependence in the relationships between the wave height and the water column parameters (Fig. 6). The first panel shows the cross-correlation between the cosine-corrected wind speed and the wave height. There was no significant

Table 1. Pearson's correlation coefficients (r) and Bonferroni's adjusted probabilities (p) for selected time series data

	Wave height		Suspended solids		POM	
	r	p	r	p	r	p
Suspended solids	0.67	<0.001				
POM	0.50	<0.001	0.77	<0.001		
Percent organic	−0.27	0.028	−0.50	<0.001	0.02	1.000

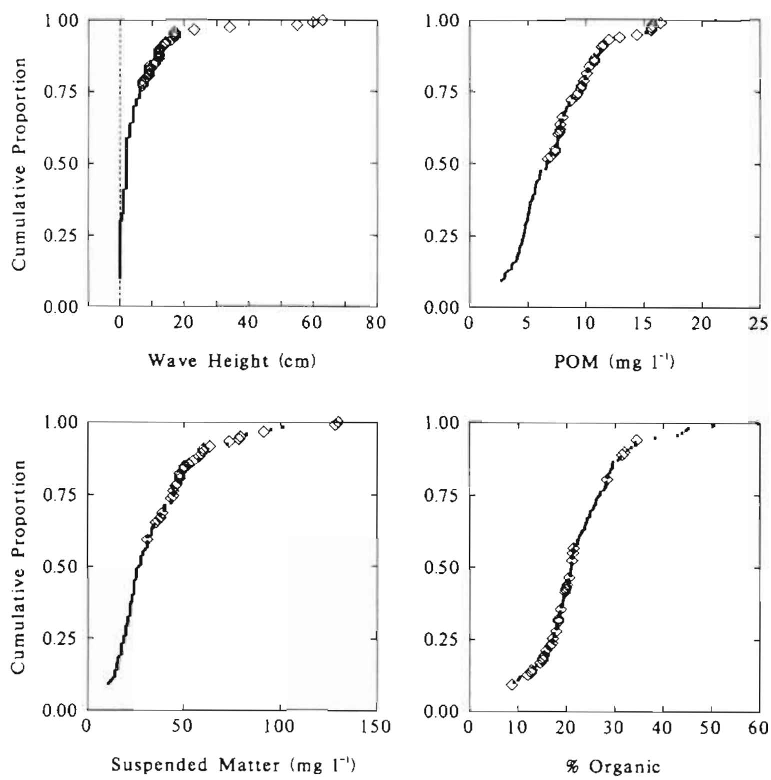

Fig. 3. Quantile plots of the daily sampling data. Observations associated with waves of 7 cm or greater in height are plotted with a diamond. In these plots, an 'S' shape is characteristic of a symmetrical distribution. Note that larger waves are associated with high suspended solids (lower left panel) and POM concentrations (upper right), but they are also associated with low percent organic (lower right)

correlation at lags other than zero. The suspended solids and the POM were significantly correlated with the wave height on the previous day, but the correlation rapidly decreased. The plot of the wave height versus the percent organic shows that there was no significant correlation at lags other than zero. The cross-correlations show that the 2 parameters making up the percent organic were significantly correlated with the wave height at non-zero lags, but the percent organic itself was not.

Clam growth results

Following the recovery of the implanted clams, we used the initial and final shell parameters to calculate the average daily growth rate. We performed microgrowth analysis on all clams recovered from the first and second implant groups. The amount of shell growth in the third group was too small to allow the use of this technique. Table 2 shows the average growth and water column parameters for the 3 implantation periods. Note that conditions were similar for the first 2 implantations, as was the average daily microgrowth. Because of the inclusion of the preliminary period in the caliper shell growth in

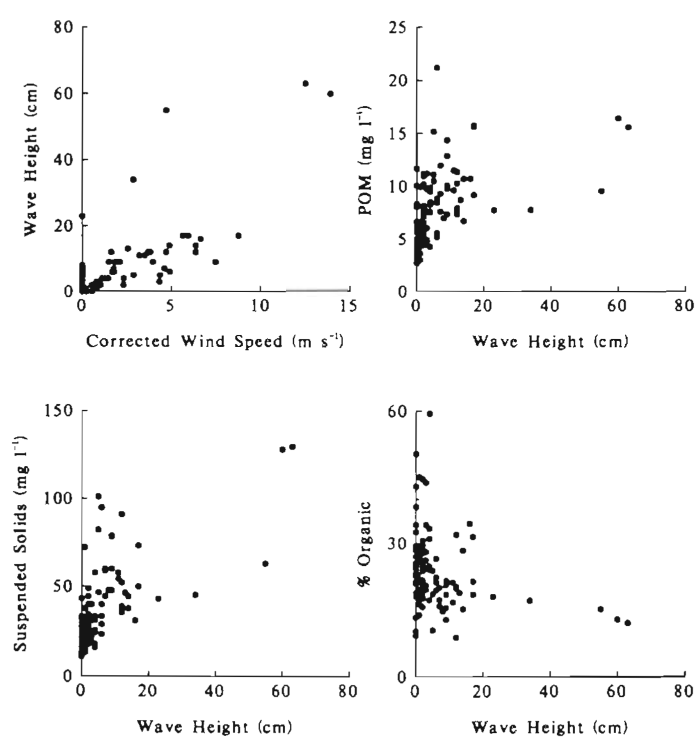

Fig. 4. Plots of wind speed and water column parameters versus the wave height. As the wave height increases, the suspended solids and POM concentrations increase and the percent organic decreases

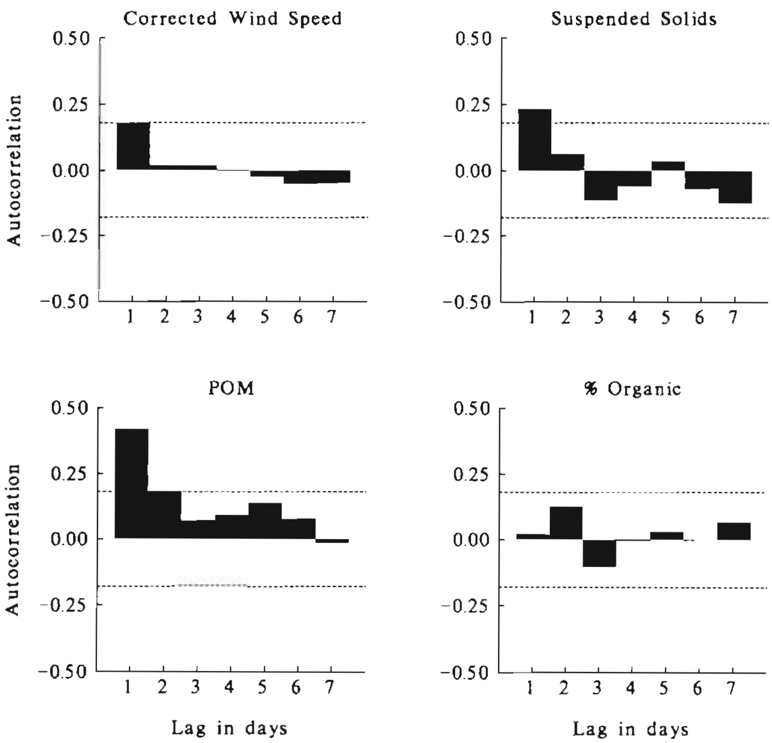

Fig. 5. Plot of the autocorrelation function of selected time series data. The dotted line represents the 95% confidence interval (Chatfield 1984). There is significant autocorrelation at a lag of 1 d in the wind speed and the suspended solids. The POM is significantly autocorrrelated at lags of 1 and 2 d. There is no significant autocorrelation in the percent organic data

Total suspended solids was significantly correlated with individual growth in the first implant group, but not the second.

The relationship between the ensemble daily microgrowth and the percent organic of the suspended solids is presented graphically in Fig. 7. Standard errors of the ensemble daily growth rate for any day ranged from 4 to 13 µm d^{-1}. Fig. 8 is a scatterplot of the ensemble daily growth for the 2 groups versus the percent organic of the seston. The plots show that as the percent organic increased, growth increased. The relationship was statistically significant, but it accounts for less than half of the variability, <45%, as assessed by squaring the correlation coefficient for the ensemble growth increment series. The explained variability was even less, on average, for the individual growth series.

We also explored the time dependence in clam growth using autocorrelation. For example, conditions in the water column (e.g. percent organic) on one day may influence growth on the next. There was no significant autocorrelation in the ensemble growth data at any lag, implying

the first group it is difficult to compare these measurements to the microgrowth measurement. Group 3 had similar seston values to the first 2 periods but lower water temperatures, higher wave heights and lower percent organic.

Table 3 shows the Pearson's correlation coefficients between the daily microgrowth data and the water column parameters for the first 2 groups. Two methods were used to calculate correlation coefficients. The daily growth increments of all clams in a group were averaged: the time series of such means is termed the ensemble growth series, and correlations were calculated using this series. In addition, correlations were calculated for each individual clam's growth series. To test the significance of these correlations, values were first transformed to z ($z = \tanh^{-1} r$) and a t-test was used to determine if the mean z was significantly different from zero (Zar 1984). The mean value of the individuals' r-values and the significance of the t-test on z are reported in Table 3. The table shows that both the ensemble and individual growth series were significantly correlated with the percent organic of the seston for both implant groups. However, the r-values were much higher for the ensemble growth values, indicating that there was a great deal of individual variability.

Table 2. *Mercenaria mercenaria*. Summary statistics for the seston and growth data obtained over the 3 implantation periods. The microgrowth means and standard deviations were taken from the ensemble growth series. Microgrowth data was not collected for the third implant group. Caliper growth data represents measurements over a longer time period than the microgrowth measurements for Group 1

	Group 1		Group 2		Group 3	
	Mean	SD	Mean	SD	Mean	SD
Days	34	-	63	-	21	-
Water temp. (°C)	23.6	12.0	14.6	4.1	8.3	2.2
Wave height (cm)	3.5	3.1	6.6	11.2	8.4	2.2
Suspended solids (mg l^{-1})	39.1	22.4	35.4	21.8	36.1	27.0
POM (mg l^{-1})	8.7	3.7	7.4	3.0	6.5	3.7
Percent organic	24.5	7.6	24.1	9.3	19.8	6.3
Clams recovered	15	-	16	-	23	-
Caliper growth (µm d^{-1})	111.1	39.9	43.5	23.2	0.7	2.1
Microgrowth (µm d^{-1})	95.4	9.3	85.7	10.6		

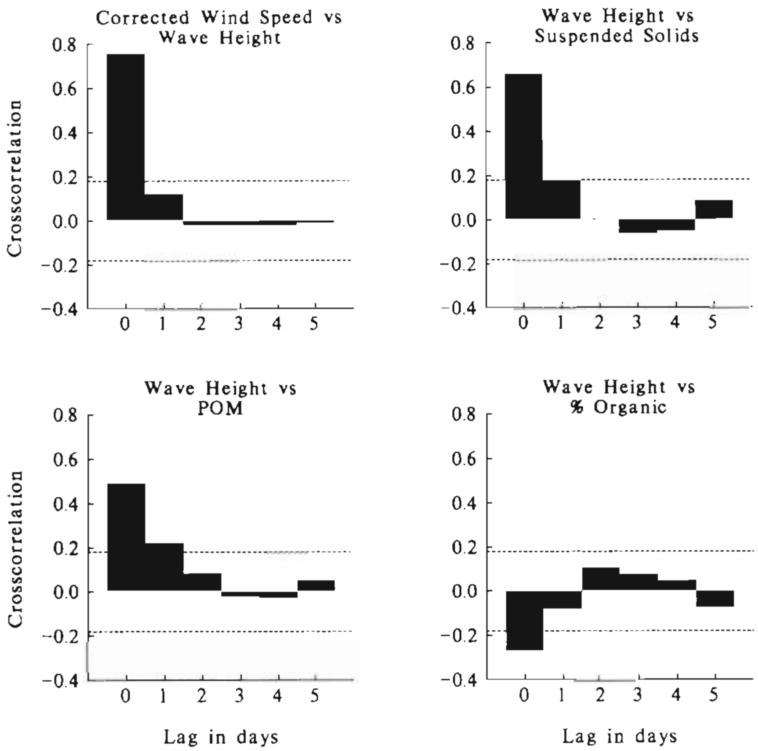

Fig. 6. Plot of the cross-correlation function of selected time series data. The dotted line is the 95% confidence interval (Chatfield 1984). Of the water column parameters, only the suspended solids and POM are correlated to the wave height at non-zero lags

that growth was not correlated with previous growth. The probabilities were >0.10 and 0.50 for Groups 1 and 2 respectively at a lag of 1 d. There was also no cross-correlation with the percent organic at lags other than zero. The cross-correlation at lag zero is of course equal to the value found in Table 3 and the probabilities at a lag of 1 d were >0.50 and 0.30 for Groups 1 and 2 respectively. Thus, clam growth was not significantly correlated to prior conditions in the water column. In our results, growth was only demonstrably related to the daily conditions in the water column as measured by the percent organic, and there was no lag or memory in the growth rate response.

DISCUSSION

The results show weather-induced changes in the seston and that the growth of the implanted clams responded rapidly to this variability.

Weather effects

The time series data show a great deal of variability in the water column parameters at this site. Most of the time conditions were placid; waves were below 7 cm in height more than 75% of the time. During the other 25%, conditions were much more energetic, above the estimated threshold for the movement of the bulk sediment. These periods were responsible for increases in the suspended load as well as the POM. There was also a reduction in the percent organic associated with larger waves (see Fig. 4). This dependence of the water column parameters on the wind and wave field has been shown before (Miller & Sternberg 1988, Emerson & Grant 1991, Fegley et al. 1992). In addition, Miller & Sternberg (1988) correlated peak wave velocities with rapid increases and then a gradual (tens of seconds) decrease in the suspended load for individual waves. The local weather appears to be forcing the conditions in the water column at Cape Henlopen and other intertidal sites.

There is a potential bias in sampling the water column parameters at one time point in a day, especially if sampling failed to coincide with endogenous rhythms in feeding and growth. The results of Fegley et al. (1992) show that the within day variability can be as large as the yearly variability. However, there are important differences between their site and ours that are rele-

Table 3. *Mercenaria mercenaria*. Pearson's correlation coefficients (r) and Bonferroni's adjusted probabilities (p) for the clam growth data. For an explanation of the 2 methods used see the text. Shell growth is significantly correlated to the percent organic for both the ensemble and individual daily growth series (n = 15 and 16 clams for Groups 1 and 2 respectively)

	Group 1 (34 d)				Group 2 (63 d)			
	Ensemble growth		Individual growth		Ensemble growth		Individual growth	
	r	p	Avg r	p	r	p	Avg r	p
Water temp.	0.03	1.0	0.02	1.0	−0.06	1.0	−0.03	1.0
Wave height	−0.13	1.0	−0.06	0.88	−0.01	1.0	−0.01	1.0
Solids	−0.31	0.45	−0.15	0.01	−0.21	0.61	−0.09	0.1
POM	−0.03	1.0	−0.01	1.0	0.09	1.0	0.02	1.0
Percent organic	0.66	<0.001	0.32	<0.001	0.51	<0.001	0.18	<0.001

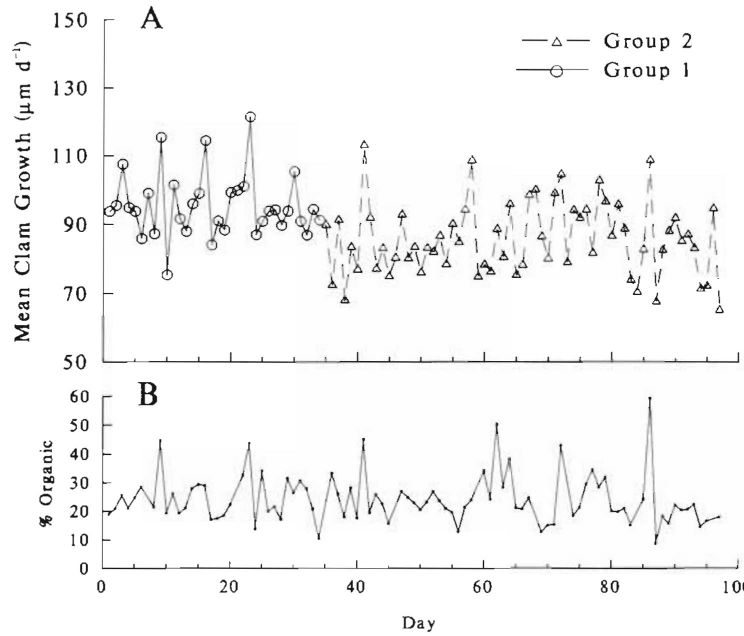

Fig. 7. *Mercenaria mercenaria*. Time series plots of the ensemble daily growth series and the percent organic of the seston

vant here. Their site had a large tidal component in the fluid velocities, ranging from 0 to almost 240 cm s^{-1}. Our site is located on a large intertidal sandflat with a much smaller tidal influence. We measured tidal components in fluid velocities ranging from undetectable to ~10 cm s^{-1}, below the threshold required to erode the sediment (Bock 1992). These values agree with the finding of Ray (1989) at the same site. Except in calm weather, wave generated fluid motion predominated over the tidal component. We also found small differences between low-tide and high-tide seston parameters, with among day variability being much larger than within day variability. In the present study, the finding of a 1 d lag in the seston autocorrelation functions (Fig. 5) suggests daily sampling adequately characterized important variations in seston. Although continuous measurements would undoubtedly be superior, we believe that the water column data collected at a single time point during the day is adequate in quantifying seston variability at this site, although this may not be true at other sites (e.g. Fegley et al. 1992).

The autocorrelation in the POM and the cross-correlation between wave height and POM suggests that the concentration of the organic fraction was partially dependent on previous conditions, including the wave intensity. Since the suspended solids and POM covary similarly, the ratio between the two (the percent organic) showed no temporal pattern with little autocorrelation or cross-correlation with the wave height in the percent organic data. Since the percent organic was significantly and negatively correlated with the total suspended solids and not the POM (Table 1), it varied in response to dilution with the inorganic fraction. This type of dilution effect has been described before (e.g. Anderson & Meyer 1986).

Local conditions can change on a wide range of time scales: seasonally in response to productivity, semi-monthly in response to spring and neap tides, daily in response to the local weather, hourly in response to the tides, and seconds in response to individual waves. Spectral analysis of the data set revealed no strong patterns at longer time scales (e.g. semi-lunar and lunar). The autocorrelation and cross-correlation in the data described above give some insight into the dynamics of Breakwater Harbor. One can deduce that the system has a large wind-driven component, with the breakwaters and Cape Henlopen isolating the system from the Delaware Bay as a whole. Waves are formed by the local wind field and wave-induced resuspension is responsible for a large portion of the suspended solids at the study site. Since there is no detectable lag between wave height and suspended solids concentrations, suspended load concentrations responded to waves in less than a day, the sampling period used here.

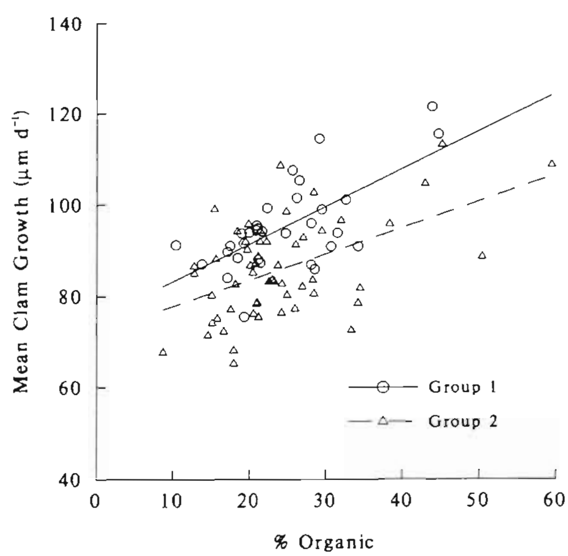

Fig. 8. *Mercenaria mercenaria*. Scatterplot of the ensemble daily growth rate versus the percent organic of the seston. The 2 lines show a linear fit of the growth increment to the percent organic: Group 1 = 0.82 × %organic + 75; Group 2 = 0.57 × %organic + 72

Factors affecting growth

The growth rates and magnitude of the variability seen in these experiments compare favorably to those found in the literature. Average growth rates of 100 µm d^{-1} were reported by Hibbert (1977). In a study involving predator exclusion, Craig et al. (1988) measured growth rates reaching 167 µm d^{-1}. In an implantation experiment, Turner & Miller (1991b) measured individual growth rates ranging from 40 to 210 µm d^{-1}. Some studies measure shell growth as a length increase as measured on the longest anterior to posterior axis (e.g. Ansell 1968, Hibbert 1977, Peterson et al. 1984, Craig et al. 1988). In contrast, this study measured growth along the shell's axis of maximum growth (e.g. Turner 1990, Turner & Miller 1991b). In our study, growth measurements along the length axis were about 5% greater than those along the axis of maximum growth. The mean microgrowth rates and the variability in the growth rates measured here compare well to the findings of other researchers (Turner & Miller 1991b). However, it is difficult to directly compare caliper and microgrowth values, even if made along the same dimension. Calipers measure in a plane though the shell; such values represent growth projected in a dimension on that plane. In contrast, microgrowth measurements are made across lines of growth within the shell at an angle to conventional shell dimensions.

We compared the environmental parameters and clam growth to determine what factors influenced growth. The results show that there was no significant correlation between the daily growth increment and the water temperature. Since temperature has been shown to affect clam growth, the lack of a relationship could be because the water temperature remained within the clams' tolerance limits. Temperatures below 8°C have been shown to dramatically reduce clam growth (Ansell 1968). The low growth in the third implant group is most likely due to low temperatures (Fig. 2, Table 2). The percent organic was the only water column parameter showing a consistent and highly significant correlation to clam growth. As this percentage increased, the shell growth increased (Fig. 8). It is possible that other relationships in the growth data were obscured by the correlation between growth and percent organic. To test for other correlations while controlling for percent organic, we performed a partial correlation analysis (Zar 1984). This yielded no new significant correlations with any of the remaining seston variables. The lack of a relationship between wave height and growth suggests that fluid flow alone had little direct influence on growth at the study site. These results make it possible to examine hypotheses concerning the factors affecting growth.

The feeding activities of bivalves may reduce the concentration of phytoplankton in the boundary layer (e.g. Wildish & Kristmanson 1984, Fréchette et al. 1989). It is likely that the density of clams used here (30 m^{-2} in an isolated patch) and the magnitude of fluid flow minimized any potential depletion. Although boundary layer depletion was not considered here, it has been implicated at other sites (e.g. Peterson & Black 1987).

Growth could be reduced by an increase in the suspended inorganic matter due to interference with either feeding or digestion. In this study it is impossible to differentiate between these 2 mechanisms because both predict reduced growth when there is a large amount of inorganic material in the seston. Turner & Miller (1991b) found that during simulated storms, growth was reduced and as the suspended load increased, pseudofeces production increased. They hypothesized that the production of pseudofeces significantly adds to the energetic cost of feeding, suggesting a possible mechanism of feeding inhibition.

A number of researchers contend that the quality of the food resource is important for *Mercenaria mercenaria* growth (Turner & Miller 1991b, Peterson et al. 1984). Although the correlation between percent organic is significant in this study, the low r-value suggests that it is not the only factor though partial correlation analyses described previously fail to suggest alternatives. The percent organic is only a gross measure of the food quality which does not consider the relative digestibility of the components of the organic pool. It is likely that additional information can be obtained by further quantifying the organic matter, the relative digestibility of the various fractions could be of considerable importance.

The flux of seston, technically defined as flow velocity × seston concentration, has been investigated and modeled for many different bivalve suspension feeders. In some cases, an increase in the flux increased the growth rate (e.g. Wildish & Kristmanson 1984, Peterson & Black 1987, Fréchette et al. 1989), and in others it decreased the growth rate (Grizzle & Lutz 1989). The model of Grizzle & Lutz (1989) predicted that shell growth is more tightly correlated with horizontal seston flux than the seston concentrations and flow alone. The models of Fréchette et al. (1989) and O'Riordan et al. (1993) show that the flux is a means of resupplying the boundary layer with food particles. The results here, and the results of Turner & Miller (1991b), suggest that the composition of the seston (e.g. percent organic) may be as important as the concentration alone. It should be possible to adapt seston flux models to account for seston composition effects by modifying the food particle sink term (e.g. O'Riordan et al. 1993) and thus model the local seston composition in a dense assemblage of suspension feeders.

These observations have shown that daily environmental variability has a strong influence on the conditions at the study site. Conditions in the water column respond quickly to the weather, changing on the time scale of 1 d or less. In 2 independent implantations, daily clam growth covaried with the percent organic of the seston. When the organic matter is diluted by the bulk sediment, more effort may be required to extract or digest it. Thus, factors unrelated to the total amount of particulate matter influence growth, and the composition of the seston may prove more important than the concentration or the flux. Clam growth responded to changes in the seston daily, with no discernible lag or memory of water column parameters. Our results underscore the importance of environmental variability on a sandflat and the rapid response of one infaunal species to this variability.

Acknowledgements. We thank K. Bock, L. Karrh and R. Karrh for their assistance with data collection on even the coldest and windiest days. We thank D. Montey of Mercenaria Manufacturing for providing the clams. Discussions with D. Thistle and W. J. Ullman proved valuable in planning, data analysis and manuscript preparation. The comments of C. H. Peterson and 2 anonymous reviewers greatly improved this manuscript. This research was supported by National Science Foundation Biological Oceanography Program grant OCE 9217020.

LITERATURE CITED

Anderson, F. E., Meyer, L. M. (1986). The interaction of tidal currents on a disturbed intertidal bottom with a resulting change in particulate matter quantity, texture and food quality. Estuar. coast. Shelf Sci. 22: 19–29

Ansell, A. D. (1968). The rate of growth of the hard clam *Mercenaria mercenaria* (L.) throughout the geographical range. J. Cons. perm. int. Explor. Mer 31: 364–409

Bayne, B. L., Hawkins, A. J. S., Navarro, E. (1987). Feeding and digestion by the mussel *Mytilus edulis* L. (Bivalvia: Mollusca) in mixtures of silt and algal cells at low concentrations. J. exp. mar. Biol. Ecol. 111: 1–22

Bock, M. J. (1992). Feeding biology and food resources on an intertidal sand flat: storm effects. M.Sc. thesis, University of Delaware, Newark

Bricelj, V. M., Malouf, R. E. (1984). Influence of algae and suspended sediment concentrations on the feeding physiology of the hard clam *Mercenaria mercenaria*. Mar. Biol. 84: 155–165

Bricelj, V. M., Malouf, R. E., de Quillfeldt, C. (1984). Growth of juvenile *Mercenaria mercenaria* and the effect of resuspended bottom sediments. Mar. Biol. 84: 167–173

Chatfield, C. (1984). The analysis of time series: an introduction. Chapman and Hall, New York

Craig, M. A., Bright, T. J., Gittings, S. R. (1988). Growth of *Mercenaria mercenaria* and *Mercenaria mercenaria texana* seed clams planted in two Texas bays. Aquaculture 71: 193–207

Dean, R. G., Dalrymple, R. A. (1984). Water wave mechanics for engineers and scientists. Prentice-Hall, Englewood Cliffs, NJ

Emerson, C. W., Grant, J. (1991). The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. Limnol. Oceanogr 37: 1288–1300

Fegley, S. R., MacDonald, B. A., Jacobsen, T. R. (1992). Short-term variation in the quantity and quality of seston available to benthic suspension feeders. Estuar coast. Shelf Sci. 34: 339–412

Fréchette, M., Butman, C. A., Geyer, W. R. (1989). The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. Limnol. Oceanogr. 34: 19–36

Grant, J., Enright, C. T., Griswold, A. (1990). Resuspension and growth of *Ostrea edulis*: a field experiment. Mar. Biol. 104: 51–59

Grizzle, R. E., Lutz, R. A. (1989). A statistical model relating horizontal seston fluxes and bottom sediment characteristics to growth of *Mercenaria mercenaria*. Mar. Biol. 102: 95–105

Hibbert, C. J (1977). Growth and survivorship in a tidal-flat population of the bivalve *Mercenaria mercenaria* from Southampton Water. Mar. Biol. 44: 71–76

Hirota, J., Szyper, J P. (1975). Separation of total particulate carbon in inorganic and organic components. Limnol. Oceanogr. 20: 896–900

Jumars, P. A., Self, R. F. L. (1986). Gut-marker and gut-fullness methods for estimating field and laboratory effects of sediment transport on ingestion rates of deposit-feeders. J. exp. mar. Biol. Ecol. 98: 293–310

Kaustky, N. (1982). Growth and size structure in a Baltic *Mytilus edulis* population. Mar. Biol. 68: 117–133

Kennish, M. J. (1980). Shell microgrowth analysis. *Mercenaria mercenaria* as a type example for research in population dynamics. In: Rhoads, D. C., Lutz, R. A. (eds.) Skeletal growth of aquatic organisms: biological records of environmental change. Plenum Press, New York, p. 255–294

Kinner, P., Maurer, D. (1978). Polychaete annelids of the Delaware Bay region. Fish. Bull. U.S. 76: 209–224

Levinton, J. S. (1991). Variable feeding behavior in three species of *Macoma* (Bivalvia: Tellinacae) as a response to water flow and sediment transport. Mar. Biol. 110: 375–383

Miller, D. C., Bock, M. J., Turner, E. J. (1992). Deposit and suspension feeding in oscillatory flows and sediment fluxes. J. mar. Res. 50: 489–520

Miller, D. C., Jumars, P. A. (1986). Pellet accumulation, sediment supply, and crowding as determinants of surface deposit-feeding rate in *Pseudopolydora kempi japonica* Imajima & Hartman (Polychaeta: Spionidae). J. exp. mar. Biol. Ecol. 99: 1–17

Miller, D. C., Sternberg, R. W. (1988). Field measurements of the fluid and sediment-dynamic environment of a benthic deposit feeder. J. mar. Res. 46: 771–796

Miller, R. G. (1981). Simultaneous statistical inference. Springer-Verlag, New York

Monismith, S. G., Koseff, J. R., Thompson, J. K., O'Riordan, C. A., Nepf, H. M. (1990). A study of model siphonal currents. Limnol. Oceanogr. 35: 680–696

Muschenheim, D. K. (1987). The dynamics of near-bed seston flux and suspension-feeding benthos. J. mar Res. 45: 473–496

Nowell, A. R. M., Jumars, P. A. (1984). Flow environments of aquatic benthos. A. Rev. Ecol. Syst. 15: 303–328

O'Riordan, C. A., Monismith, S. G., Koseff, J. R. (1993). A study of concentration boundary-layer formation over a bed of model bivalves. Limnol. Oceanogr. 38: 1712–1729

Pannella, G., MacClintock, C. (1968). Biological and environmental rhythms reflected in molluscan shell growth. J. Paleontol. 42 (Suppl. to No. 5). Paleontol. Soc. Mem. 2: 64–80
Peterson, C. H., Black, R. (1987). Resource depletion by active suspension feeders on tidal flats: influence of local density and tidal elevation. Limnol. Oceanogr. 32: 143–166
Peterson, C. H., Duncan, P. B., Summerson, H. C., Safrit, J. G. W. (1983). A mark recapture test of annual periodicity of internal growth band deposition in shells of hard clams, *Mercenaria mercenaria*, from a population along the southeastern United States. Fish. Bull. U.S. 81: 765–779
Peterson, C. H., Summerson, H. C., Duncan, P. B. (1984). The influence of seagrass cover on population structure and individual growth rate of a suspension feeding bivalve, *Mercenaria mercenaria*. J. mar. Res. 42: 123–138
Polis, D. F., Kuferman, S. L. (1973). Physical oceanography. In: Polis, D. F. (ed.) Delaware Bay Report Series, Vol. 4. College of Marine Studies, University of Delaware, Newark
Ray, A. J. (1989). Influence of sediment dynamics and deposit feeding on benthic microalgae. M.Sc. thesis, University of Delaware, Newark
Rhoads, D. C., Boyer, L. F., Welsh, B. L., Hampson, G. R. (1984). Seasonal dynamics of detritus in the benthic turbidity zone (BTZ): implications for bottom-rack mariculture. Bull. mar. Sci. 35: 536–549
Rhoads, C. C., Pannella, G. A. (1970). The use of molluscan growth patterns in ecology and paleoecology. Lethia 3: 143–161
Sleath, J. F. A. (1984). Sea bed mechanics. Princeton University Press, Princeton, NJ
Turner, E. J. (1990). Suspension feeding in oscillatory flows with resuspended bottom sediments. Ph.D. dissertation, University of Delaware, Newark
Turner, E. J., Miller, D. C. (1991a). Behavior of a passive suspension-feeder (*Spiochaetopterus oculatus* (Webster)) under oscillatory flow. J. exp. mar. Biol. Ecol. 149: 123–137
Turner, E. J., Miller, D. C. (1991b). Behavior and growth of *Mercenaria mercenaria* during simulated storm events. Mar. Biol. 111: 55–64
Wildish, D. J., Kristmanson, D. D. (1984). Importance to mussels of the benthic boundary layer. Can. J. Fish. Aquat. Sci. 41: 1618–1625
Wilkinson, L. (1990). SYSTAT manual. SYSTAT, Inc., Evanston, IL
Williams, P. J. (1985). Analysis: organic matter. In: Head, P. C. (ed.) Practical estuarine chemistry. Cambridge University Press, Cambridge, p. 160–200
Zampol, J. A., Inman, D. L. (1989). Suspended sediment measurements B: discrete measurements of suspended sediment. In: Seymour, R. J. (ed.) Nearshore sediment transport. Plenum Press, New York, p. 259–272
Zar, J. H. (1984). Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ

This article was presented by C. H. Peterson (Senior Editorial Advisor), Morehead City, N. Carolina, USA

Manuscript first received: January 26, 1994
Revised version accepted: June 29, 1994