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Determining effects of suspended sediment on condition of a suspension feeding bivalve (*Atrina zelandica*): results of a survey, a laboratory experiment and a field transplant experiment

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Abstract

The horse mussel *Atrina zelandica* (Gray) is a large, suspension feeding pinnid bivalve, common in coastal and estuarine areas of northern New Zealand. As a suspension feeder, *Atrina* is likely to be influenced by suspended sediment loads. We conducted a laboratory experiment to determine the effect of short-term elevations in turbidity levels, such as those commonly recorded during storms, on the physiological condition and clearance rates of *Atrina*. We also conducted a field survey and a 3-month transplant experiment at multiple sites along a gradient of increasing suspended sediment load in a New Zealand estuary. Laboratory clearance rates of *Atrina* declined above a threshold suspended sediment concentration, and *Atrina* physiological condition at the end of this experiment was lower in high cf. low turbidity treatments. Decreases in *Atrina* condition were detected after exposure to elevated levels for only 3 days. The field survey and transplant experiment provided empirical evidence of a strong, negative effect of increasing suspended sediment flux on the physiological condition of *Atrina*. We suggest that relationships between the physiological condition of suspension feeders and sediment settling flux could provide a link between sediment inputs, which commonly occur as a result of catchment runoff during rainfall events, and the ecological health of estuarine and shallow coastal areas. Our study also demonstrated that *Atrina* have a natural distribution limit controlled by suspended sediment load. Thus, there is potential for larger-scale functional and structural effects on benthic communities in estuarine and coastal areas with high rates of sedimentation.

Keywords: Suspended sediment flux; Condition; Transplant experiment; Field survey; Suspension feeding bivalve; Turbidity; Physiological condition; Estuary; New Zealand; Storms

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1. Introduction

Increases in sediment loads to coastal ecosystems as a result of catchment development has been recognised as a marine contaminant of considerable importance (GESAMP, 1990). Elevated sediment loading to estuarine and coastal environments can occur via urban development, forestry, farming and inadequate land management practices, and often results in elevated sedimentation rates and suspended sediment levels in estuarine and coastal waters (e.g., Ellis et al., 2000). Potentially this can translate to broader-scale changes in estuarine and coastal ecology through modifying habitats (e.g., Smith and Kukert, 1996; Saiz-Salina and Urkiaga-Alberdi, 1999) and, in particular, by influencing the health, abundance and distribution of benthic suspension feeders.

Suspended sediment concentrations in estuaries can increase significantly with sediment runoff during storm events. The majority of catchment-derived sediment entering an estuary does so during flood events associated with storms (Dyer, 1986; Hicks and Griffiths, 1992) and consequently, for short time periods (hours to several days), sediment loads can be orders of magnitude higher than normal. For example, suspended sediment levels in surface waters of a New Zealand estuary increased from background levels of 10–20 to 1000 mg/l during a storm (Fahey and Coker, 1992). Depending upon tidal conditions at the time of input, sediment will either be transported out of the estuary, or be deposited and become available for resuspension by both physical (e.g., waves) and biological (e.g., bioturbation) processes. Physical resuspension of sediments also occurs predominantly during storms (e.g., Milliman et al., 1985; De Haas and Eisma, 1993; Blewett and Huntley, 1998). Due to resuspension processes, suspended sediment levels are often even higher in bottom waters (Bricelji and Malouf, 1984; Smaal and Haas, 1997). Consequently, any impacts of elevated suspended sediment levels will be enhanced in benthic fauna, and particularly in sessile suspension feeders.

While resuspended sediments contain non-refractory particulate organic matter, which is a valuable source of food for suspension feeders (Grant, 1996), increasing concentrations of particles in the seston can also have negative effects on the feeding behaviour of suspension feeding bivalves (see recent review by Jorgensen, 1996). Increased concentrations of silts and clay in suspension may significantly increase pseudofaeces production, decrease the amount of algal food actually ingested, and may also damage bivalve gills (Morse et al., 1982; Bricelji and Malouf, 1984; Robinson et al., 1984; Stevens, 1987; Navarro et al., 1992; Willows, 1992; Iglesias et al., 1996; Navarro and Widdows, 1997). Exposure to increased concentrations of suspended sediments for an extended time could therefore result in decreased amounts of energy available for growth and reproduction, and have deleterious effects on local populations.

Laboratory experiments have indicated that suspended sediment levels as low as 100 mg/l have adverse effects on bivalve energetics (Robinson et al., 1984). Bricelji et al. (1984) also provide experimental evidence that concentrations of fine grained sediment of 44 mg/l inhibited growth of hard clams. However, particle capture and filtration rates may differ substantially in natural situations (Cole et al., 1992; Jorgensen, 1996). Extrapolating laboratory results to field situations requires simplifying assumptions as to the nature of relevant seston characteristics and laboratory experiments may incur problems with acclimation of experimental organisms to laboratory conditions (Frechette and Grant, 1991). Laboratory procedures also bypass some important spatio-temporal variability and size characteristics of seston naturally available to suspension feeders (Frechette and Grant, 1991). Hence, validating laboratory-derived responses of suspension feeders to suspended sediments using field experiments is important. To better understand how filter feeders function under field conditions, a growing body of work has studied responses to increasing concentrations of natural seston (Hawkins et al., 1996, 1999; Urrutia et al., 1996; see Special Issue of the Journal of Experimental Biology and Ecology, Vol. 219). Results suggest that continuous interrelated changes in feeding physiology can help to maintain rates of nutrient acquisition independent of short-term fluctuations in seston composition. Previous studies of responses of bivalves to natural seston concentrations often expose animals to natural seston levels in traps over weekly time scales. Such studies are important to assess responses to natural seston concentrations. Our study investigates responses of animals from in situ field sites that integrate effects over longer time scales.

The horse mussel *Atrina zelandica* (Gray) is a large, suspension feeding pinnid bivalve which is patchily distributed around the coast of northeastern New Zealand. *Atrina* are found in muddy to sandy soft sediment habitats, from shallow subtidal to about 50 m depth (Powell, 1979). They live partially buried in the substrate and protrude several centimetres above the sediment. Because of their size and their often dense and patchy distribution, *Atrina* add complex physical structure to soft sediment habitats (Cummings et al., 1998, 2001) by providing predation refuges (sensu Woodin, 1978; Dittman, 1996) and substrates for settlement of epifauna (Cummings et al., 1998). *Atrina* modify boundary flow conditions (Green et al., 1998) and have the potential to influence the estuary wide hydrodynamics and the associated transport, deposition, and entrainment of sediment. In particular *Atrina* influences both the structure and diversity of macrofaunal communities (Cummings et al., 1998, 2001).

Atrina are important suspension feeders in Mahurangi Estuary, New Zealand. The annual average sediment load to this shallow ($<$ 15 m) estuary is 52,270 tonnes per annum, 98% of which is delivered during large flood events, a value typical for estuaries (Dyer, 1986). Given the ecological importance of *Atrina* and the importance of catchment-derived sediment input as a major contaminant of New Zealand estuaries (Hicks and Griffiths, 1992), we conducted a short-term laboratory experiment to investigate whether the physiological condition of *Atrina* was affected by suspended sediments. In order to validate our laboratory experimental results we then conducted a field based survey and a 3-month transplant experiment. This approach enables us to investigate in situ responses of *Atrina* over yearly (survey) and monthly (transplant experiment) time scales. Identifying a relationship between settling flux and the physiological condition of key suspension feeders could provide a link between sediment inputs and the ecological health of estuaries and harbours.

2. Methods

2.1. Terminology

The terminology relating to the data collected by settlement traps and the *Atrina* condition measurements is provided before outlining the laboratory and field methodology.

"Suspended sediment concentration" has units of mass (or volume) of sediment per volume of water. "Net sedimentation rate" is the difference between accumulation and erosion of sediment on the seabed, and has units of mass (or volume) of sediment deposited/eroded per unit area of seabed per unit time. Thus, sedimentation rate is the difference between the rate at which sediment is being eroded from the seabed (i.e., resuspension flux) and the rate at which sediment is settling from suspension (i.e., settling flux). Resuspension flux depends on hydrodynamic conditions, geotechnical properties of the sediment, and biogenic activity within the seabed sediments. The settling flux is the product of the suspended sediment concentration and the settling velocity, which can be biologically mediated (e.g., by production of biodeposits). The settling flux is the physical measurement that is most likely to represent the effects of changes in sediment loading on the feeding activity and growth of suspension feeding animals and is what is actually measured by settlement traps. In laboratory conditions, this can be represented by a suspended sediment concentration, as there are no flow effects.

2.2. Laboratory experiment

2.2.1. Sediment

Surficial ($\leq$ 2 cm deep) sediment was collected from Cowans Bay, Mahurangi estuary (36°29′ S, 174°43′ E). The sediment was wet sieved to remove particles larger than 250 μm and washed with 1% H_2O_2 for 24 h to remove organics. The H_2O_2 was removed by 100 times dilution with seawater, and the sediment left to settle for 5 days before removal of the liquid. A 'sediment slurry' was then made by adding 25% seawater, and the slurry aerated for 24 h before sediment removal started.

2.2.2. Experimental design and set-up

The effects of different levels of suspended sediment on the clearance rates and physiological condition of *Atrina* were investigated over an 11-day period. *Atrina* were collected from Big Bay, a relatively clean water open coast site just outside Mahurangi estuary. The *Atrina* ranged from 18.1 to 22.5 cm shell length. Four individuals were immediately frozen for physical and biochemical condition analyses, respectively. Twenty-one 25-l aquaria were filled with 15 l of seawater and continually aerated. Two *Atrina* were placed in 18 of the aquaria, and allowed to acclimatise for 24 h. *Atrina* were held in their natural orientation on the floor of the aquaria with mesh baskets. Temperature was held constant at 17 °C, and a 10:14 light:dark cycle was used.

Seven treatments were used in the experiment (Table 1). Sediment levels used were chosen to cover a range of natural concentrations of sediment input recorded in Mahurangi estuary and similar New Zealand estuaries. In many estuaries there is a natural background of 10–20 mg/l of suspended sediment present at all stages of the tide (Dyer, 1986; Fahey and Coker, 1992). During and immediately following storm events, these levels can become considerably elevated, reaching extremes of up to 1000 mg/l in surface waters (Fahey and Coker, 1992). Background turbidity levels measured throughout the year in Mahurangi estuary range from 1.30 to 22.9 FTU (Formazin Turbidity Units) (October 1998); 1.40 to 16.3 FTU (April 1999); 1.2 to 9.2 FTU (January 1999). These levels equate to suspended sediment concentrations of between 12 and 90 mg/l. Thus, we chose

Table 1
Summary table showing the treatments used in the experiment, and the volume of sediment added to each aquaria twice daily, and the turbidity reading of this volume of sediment in 15 l of clean seawater

Treatment	Sediment added (volume of slurry in 120 ml) (ml)	Turbidity reading of sediment slurry (FTU)
A	10	30
B	20	60
C	40	120
D	80	240
No sediment	None	< 5
Sediment only	40	120
3-day	114	

turbidity levels to reflect both background and storm-associated suspended sediment concentrations (i.e., 23–512 mg/l; Table 1). The experiment also included control treatments: i.e., a 'no sediment' treatment with *Atrina* and without sediment addition, and a 'sediment only' treatment (i.e., without *Atrina*, and with an identical sediment addition as treatment C) to control for natural settlement of sediment from the water column. As the length of time suspended sediment levels remain elevated varies, we also included a treatment to which sediment was added for the first 3 days of the experiment only (i.e., 3-day, Table 1). Each treatment was replicated in three aquaria using a complete randomised block design.

The volume of sediment slurry required for each treatment was made up to 120 ml with seawater, and added to each aquaria twice daily (at 8 a.m. and 8 p.m.) throughout the experiment. A total of 120 ml of water was removed from each aquaria at both 8:30 a.m. (i.e., half an hour after addition of the sediment slurry) and 1:30 p.m. (i.e., 5.5 h after sediment slurry addition), and subsequently measured for turbidity (using a Model 2100A Hach Turbidimeter). The *Atrina* were fed 1 ml of *Chaetoceros* (3–6 μm cell size) and 1 ml of *Isocrysis* (10–14 μm) twice daily, at the same time as the sediment slurry was added. Temperature and dissolved oxygen were measured daily throughout the experiment using a Yellowsprings Instruments Model 55 DO Meter.

2.2.3. Estimation of Atrina clearance rate

The volume of water cleared of suspended particles per unit time (i.e., clearance rate, CR) per individual was calculated as follows:

$$\mathrm{CR}\ (\mathrm{l/h}) = [\mathrm{volume/time} \times (T_1 - T_2)/T_1]/N$$

where volume = 15 l, time = 5 h, N = number of individuals and T_1 and T_2 = turbidity (FTU) 0.5 and 5.5 h after sediment addition, respectively. CRs were corrected for natural sedimentation (calculated as mean percent loss of turbidity in the sediment only treatment).

2.2.4. Assessment of Atrina physiological condition

At the end of the experiment, one *Atrina* from each aquaria was used to determine physical condition, and the other to determine biochemical condition. Physical condition was determined by removing the *Atrina* flesh and drying at 60 °C to constant weight. The ratio of dry flesh weight to shell length (hereafter '$CI_{flesh:length}$') was used as an index of *Atrina* physical condition. The biochemical condition index used was the ratio of flesh glycogen content to shell length (hereafter '$CI_{glycogen:length}$'). These indices are modifications of those used by Roper et al. (1991), to determine oyster condition. The glycogen content of *Atrina* flesh was determined by adding the flesh to a 50-ml mixture of chloroform:methanol:water (2:4:1, v/v) and homogenising using an Ultra-tunaxmixer. After centrifugation at 2000 rpm for 10 min, the centrifugate was removed and the residue extracted with a further 50 ml of solvent mixture. This step was repeated twice. The residue was then dried at 60 °C for 48 h and weighed as the polymeric fraction containing polymeric carbohydrate as glycogen and protein (= polymeric dry weight; Whyte and Englar, 1982). A total of 100 mg of the dried polymeric fraction was hydrolysed with 2 mol/l H_2SO_4 at 100 °C for 2 h. The hydrolysate was then made up to 50 ml with deionised water and homogenised. Subsamples (0.1 ml) were analysed, in triplicate, for carbohydrate using the phenol-sulphuric acid procedure (Dubois et al., 1956) with D-glucose as the standard. Glycogen values were then obtained by multiplying the equivalent glucose values by 0.90. These physical and biochemical condition indices were also calculated for the *Atrina* collected from Big Bay at the beginning of the experiment.

2.2.5. Statistical analyses

All data were initially tested for normality (Shapiro–Wilk test) and homogeneity of variance (F max test). Where necessary, data were rank-transformed. When significant differences were detected, the actual differences between treatments were determined using Students–Neuman–Kewells (SNK) or Tukeys comparison of means (for untransformed or rank transformed data, respectively).

Differences in temperature, dissolved oxygen and turbidity between treatments during the experiment were assessed using repeated measures ANOVA (Crowder and Hand, 1990), with treatment as a fixed factor and block as a random factor.

Differences in clearance rate between treatments over the experiment were also investigated using ANCOVA, with treatment as a fixed factor, to determine whether slopes and intercepts of any relationship with time were affected by the treatment levels. To investigate this relationship further, data were re-analysed as a response surface, using a second-degree polynomial. The 3-day treatment was not included in either analysis, as the marked change in clearance rates of this treatment once the sediment addition stopped at the end of Day 3 (see Results) would have confounded the regression analysis.

To determine whether the condition of the *Atrina* deteriorated under our laboratory conditions, the condition of *Atrina* in the 'no sediment' treatment was compared with that of *Atrina* collected at the beginning of the experiment, using a Student's t-test. A t-test was also used to compare the condition of *Atrina* from the 3-day treatment with those in the no-sediment treatment. Linear regressions were used to assess the effect of increased sediment concentration on condition of *Atrina* over all treatments.

2.3. Field survey

Ten sites where chosen in Mahurangi Estuary (Fig. 1) to assess the physiological condition of *Atrina* and suspended sediment flux. Sites were selected to encompass the

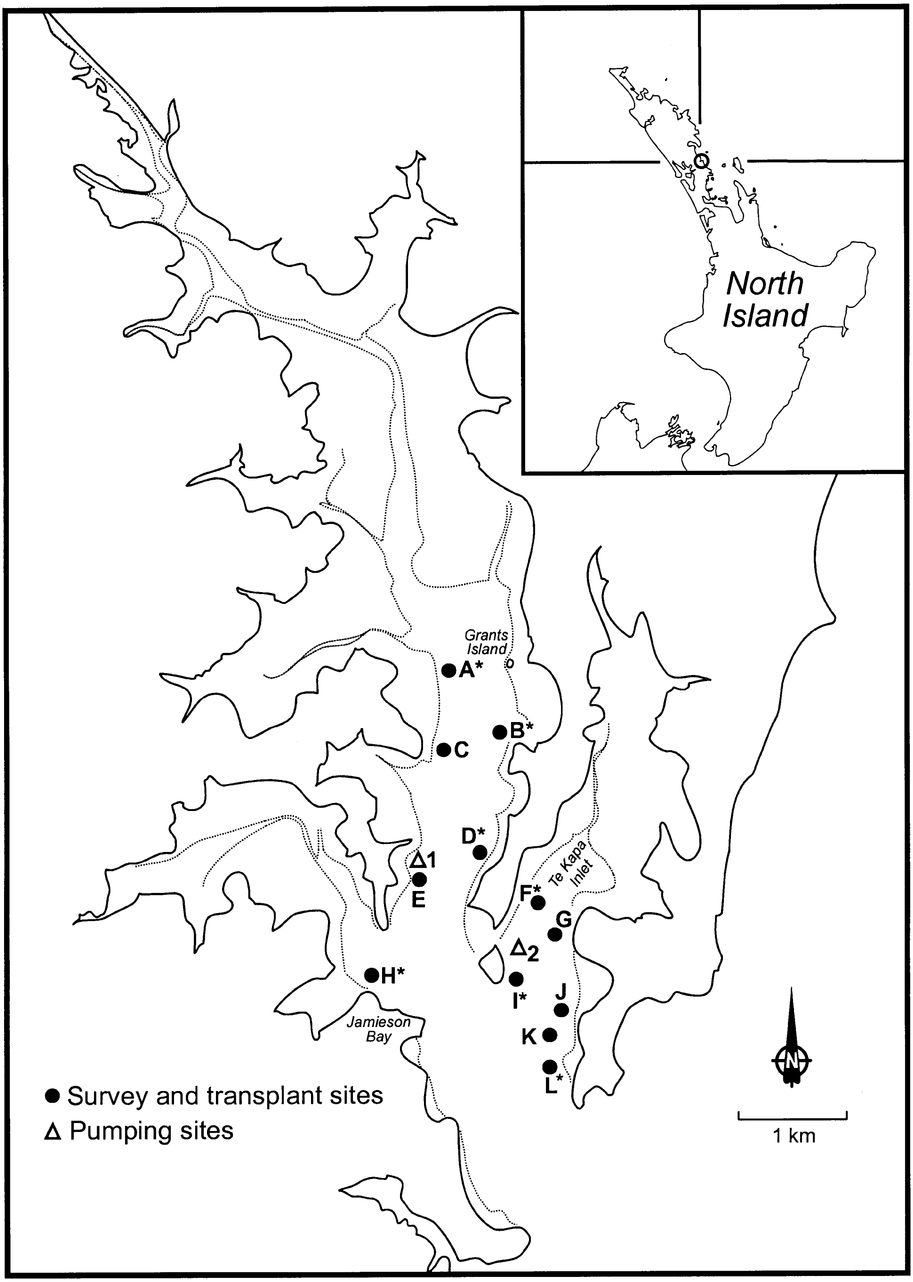

Fig. 1. Mahurangi Estuary, showing the locations of the sampling sites and the two sites used for the pumping experiment. The transplant sites are indicated by the symbol *. Sites are identified by letters, with A furthest up the estuary and L closest to the mouth.

extent of the natural *Atrina* distribution within the estuary and to reflect a wide range of variation in sedimentation rates. Suspended sediment levels increase with distance up the estuary and, correspondingly, the substrate type becomes increasingly composed of fine silts and mud. *Atrina* are found naturally from Grants Island south (Fig. 1). Each site was located within a natural bed of *Atrina*, although the uppermost sites in both the main body of the estuary and Te Kapa Inlet were essentially located at the boundary of the animals distribution and densities were very low. Seafloor sediments at the sites were very muddy, with the exception of Sites E and L, which consisted of sandy mud. Sites varied in depth from 3.3 to 7 m. Salinity varied between 33‰ and 35‰, with variance being recorded between sampling times rather than sites. Temperature varied between sampling dates from 15 to 23 °C, with a temperature difference of 1 to 1.5 °C recorded between sites on any one date. Therefore, there were no salinity or temperature gradients down the estuary.

Sites were established and sediment traps (see below) deployed on 7–8 January 1998. Traps were sampled three times, at approximately monthly intervals (i.e., 3rd February, 11th March, and 7th April 1998). On the last sampling occasion, 30 *Atrina* were collected from each site to assess physical (20 individuals) and biochemical (10 individuals) condition. As a result of very low natural *Atrina* densities at Site G, only biochemical analysis was conducted.

At each site three water column and three seafloor sediment traps were deployed to determine the settling flux of suspended sediment. The mouth of each water column trap was positioned 50 cm above the seabed, while the seafloor traps were buried in the sediment so that the mouth was positioned about 8 cm above the bed. Thus, the seafloor traps sampled at about the same height as the top of the resident *Atrina*. Sediment traps were 50 cm long and were made of stainless steel tubing with an internal diameter of 5 cm and an aspect ratio of 10:1. Studies of the performance of sediment traps with different aspect ratios indicate that settled sediment collected in the traps would not be resuspended (Hargrave and Burns, 1979; Baker et al., 1988; Butman et al., 1986; Gardner, 1980a,b). Preservatives were not added to the sediment traps on deployment because this can radically alter estimates of sediment organic matter due to the death and decomposition of animals that may swim into traps (Hedges et al., 1993). To assess the collection efficiency (i.e., whether the material caught in the traps was actually the same as that suspended in the water column), a 12-h experiment was conducted at two different sites on 7 April 1998. This involved pumping water from 8 and 50 cm above the seafloor and characterising the suspended sediment collected and Chlorophyll *a*. The experiment demonstrated that the median particle size in the sediment traps and pumped samples were very similar (Table 2).

Of the three replicate traps, sediment from one was used to measure sediment dry weight, and sediment from a second was used to measure sediment particle size and organic content. The third replicate was used as a backup for the first two. All samples were preserved on collection in a solution of mercuric chloride (about 40 ppm). A Galai particle analyzer (Galai Cis–100: Galai Productions, Migdal Haemek, Israel) was used to measure sediment particle size (as % number of particles found in the 2 μm size classes). One of the advantages of using the Galai particle analyser is the ability to measure sediment grain size characteristics either on the basis of % particle volume or % particle

Table 2
Comparison of mean sediment trap measurements with water pumped from 8 and 50 cm above the sea floor

Site	Height above seafloor (cm)	Pumping experiment		Chlorophyll *a* (μg/l)	Sediment traps	
		Organic content (%)	Median particle size (μm)		Organic content (%)	Median particle size (μm)
1	8	15.4	3.0	1.43	9.5	3.0
1	50	18.3	3.5	1.49	15.3	3.0
2	8	11.7	3.7	1.34	8.3	3.0
2	50	20.81	4.0	1.58	6.2	4.0

number. In this study we have used particle number because this is more closely related to the way the bivalves handle sediment particles and particle size analysis is not unduly biased by a few large particles. Organic content was measured as loss on ignition (400 °C for 6 h) as a relative measure of organic carbon, and expressed as a % of the total sediment collected in traps.

Atrina condition was measured using two condition indices. Physical condition was assessed as the ratio of flesh dry weight (after drying at 60 °C for 48 h) to shell length. Biochemical condition was measured as the ratio of polymeric dry weight to shell length. Polymeric dry weight was determined as described for the laboratory experiment. Glycogen was not measured as we expected the effects to be stronger in field conditions due to the longer time frames of exposure.

2.4. Transplant experiment

To determine that the response observed from field measurements of *Atrina* was due to differences in sediment settling flux around the estuary, rather than population differences, a 3-month transplant experiment was conducted. Seven sites for the transplant were selected in the vicinity of those used in the survey (Fig. 1). The sites were chosen to reflect a wide range of sediment regimes and varied in depth from 3 to 7 m. With the exception of Site A, *Atrina* were found naturally at all sites. *Atrina* (average shell length = 22.5 cm) were collected from a single site where suspended sediment flux was relatively low (Site L; Fig. 1) by SCUBA divers. Forty individuals were then transplanted into a 1 m^2 experimental plot at each site, including Site L. *Atrina* were collected and transplanted on the 20th and 21st July 1998. The transplanted *Atrina* were left undisturbed for 3 months (i.e., until October 28th 1998) at which time they were removed and their physiological condition assessed. Shell lengths of 30 transplanted *Atrina* from each site were measured at the beginning and end of the experiment. Physical condition (dry weight: shell length) of 10 *Atrina* from each site was determined. In addition, biochemical condition (i.e., polymeric dry weight) of 5 *Atrina* from Sites L, A and F was also measured. Condition was determined using methods described for the laboratory experiment. Physical condition was also determined on 10 individuals from the collection site (L) at the start of the experiment. Physical condition was concentrated on in this experiment as when length is confined to a small range and is known initially, an increase in physical condition signifies an increase in flesh biomass.

Sediment settling flux was measured at each site throughout the study, using calibrated sediment traps. At each site, two water column sediment traps were deployed. In the field survey we found no significant difference in the particle size or organic content of the sediments collected by water column versus bedload traps (Table 2), therefore only water column traps were used. The mouth of each water column trap was positioned 50 cm above the seabed. Traps were deployed at two corners of the 1 m^2 experimental plots, positioned diagonal to the main tidal flow to minimise any potential flow artefacts. Traps were sampled three times during the experiment, at approximately monthly intervals (i.e., 20th August, 22nd September and 28th October 1998). Of the two traps deployed at each site, sediment from one was used to measure sediment dry weight, while sediment from the second was used to measure sediment particle size and organic content (using methodology discussed for the field survey).

3. Results

3.1. Laboratory experiment

3.1.1. Temperature and dissolved oxygen

Over the course of the experiment, water temperatures ranged from 17.3 to 16.8 °C, and no significant differences between treatments were detected ($P > 0.05$). Dissolved oxygen (DO) always exceeded 80% during the experiment, and the only treatment effect was recorded on Day 9, when the ‘sediment only’ treatment had very slightly higher levels than the 10-ml sediment addition treatment (i.e., 98.83% cf. 98.07%, respectively; $P = 0.0397$). While some significant differences in temperature and DO were detected between blocks, these differences were also very small (i.e., 0.5 °C; 2.5%).

3.1.2. Turbidity

A significant time × treatment interaction ($P = 0.0001$) was detected in the repeated measures ANOVA, thus data were analysed separately for each time. Turbidity differed significantly between treatments throughout the experiment (Fig. 2), both 0.5 h after the addition of sediment and 5 h later ($P < 0.05$). As expected, turbidity levels were generally highest in the ‘sediment only’ treatment and lowest in the ‘no sediment’ treatment (Fig. 2). From Day 5 onwards, the ‘sediment only’ treatment turbidity was significantly higher than all other treatments (Fig. 2). The turbidities of the ‘3-day’ treatment were similar to those recorded in the ‘sediment only’ and 80 ml treatments on Days 1 and 3; however, once sediment addition stopped, turbidity levels decreased to those observed in the ‘no sediment’ treatment (Fig. 2).

As the experiment progressed, the turbidity levels in the treatment without *Atrina* (i.e., sediment-only) increased, and by the end of the experiment they were more than eight times higher than on Day 1. This magnitude of increase did not occur in the sediment addition treatments with *Atrina* (Fig. 2), indicating the *Atrina* were processing the sediment and removing it from the water column, thus reducing the turbidity levels. Turbidities of the no-sediment treatment remained low, as did those from the 3-day treatment once the addition of sediment to this treatment had ceased after Day 3

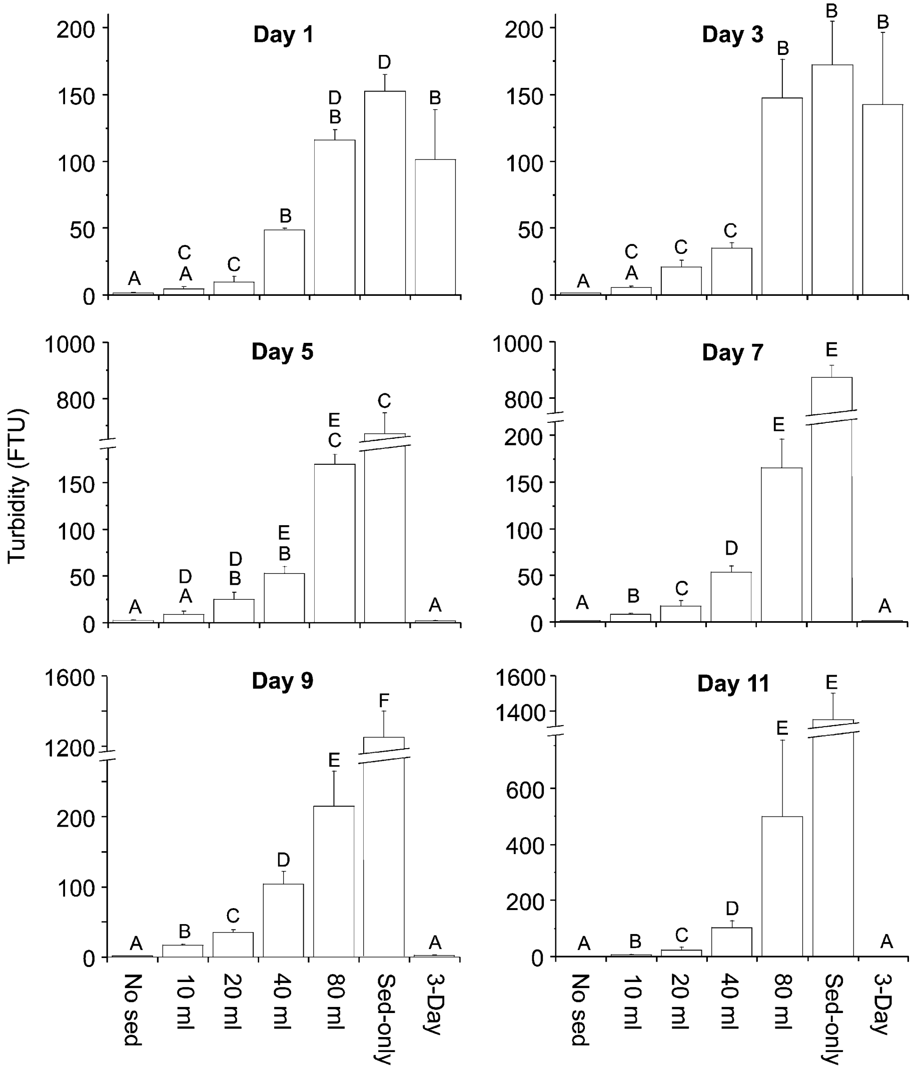

Fig. 2. Turbidity levels (mean ± standard error) measured in each treatment over the experiment. Letters above bars show significant differences between treatments detected using ANOVA (as given by Tukeys comparison of means for rank transformed data); treatments with the same letter are not significantly different from each other. 'No sed' = *Atrina*, no sediment addition; 'sed-only' = without *Atrina*, 40 ml of sediment added; '3-day' = *Atrina*, sediment added for the first 3 days of the experiment only.

(Fig. 2). There were interesting differences in how the turbidity levels of any particular treatment changed over the course of the experiment (Fig. 2). While the turbidities of the sediment addition treatments generally doubled between Days 1 and 11, those in the highest dose sediment treatment (80 ml; treatment D) showed a four-fold increase.

3.1.3. Atrina clearance rate

Suspended sediment addition increased *Atrina* clearance rates. The lowest clearance rates were observed for the *Atrina* from the no-sediment treatment (mean clearance rate range = 0.15–0.57 l/h). *Atrina* in the lower sediment-dose treatments (i.e., 10 and 20 ml; treatments A and B, respectively) had the highest clearance rates throughout the experiment (mean clearance rate ranges = 0.70–1.10 and 0.61–0.95 l/h, respectively).

As the experiment progressed, all of the sediment addition treatments showed declines in clearance rates. Treatments A and B (10 and 20 ml, respectively) had similar rates of decline (the slopes of their regression models were almost identical; Fig. 3), while treatment C, the next highest sediment dosed treatment at 40 ml, showed a much faster decline (Fig. 3). In the latter case, the clearance rate almost halved between the beginning (mean clearance rate on Day 1 = 0.87 l/h) and end (mean clearance rate on Day 11 = 0.49 l/h) of the experiment. The clearance rates of the highest dose sediment treatment D (80 ml) were low from Day 1 (mean = 0.61 l/h), and consequently showed the smallest decline with time of all the sediment addition

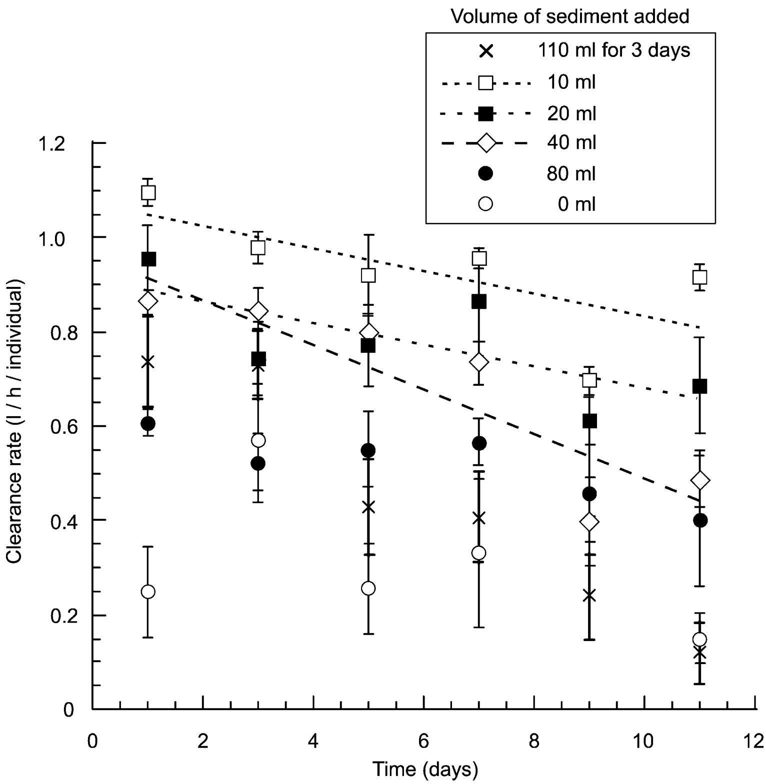

Fig. 3. Regression of change in clearance rate of *Atrina* from the sediment addition treatments over the experiment. 10 ml treatment $R^2 = 0.32$, 20 ml treatment $R^2 = 0.17$, 40 ml treatment $R^2 = 0.62$.

treatments (Fig. 3). The 3-day treatment clearance rates were similar to those of the sediment addition treatments early in the experiment (0.74 l/h), but after 3 days (when the sediment addition stopped) they declined to levels similar to those of the 'no sediment' treatments (0.20–0.40 l/h).

The overall ANCOVA detected a relationship between clearance rate and time ($P=0.0001$). It also detected a treatment effect; i.e., the intercepts of the relationships with time differed with treatment ($P=0.0001$). However, this analysis did not detect an overall difference in the slopes of the regression lines ($P=0.3899$). The response surface analysis detected highly significant experimental effects of time ($P=0.0023$), ml of sediment added ($P=0.0003$) and (ml of sediment added)^2 ($P=0.0001$) (Fig. 4). The resultant surface map shows that the model predicted *Atrina* clearance rates would increase with increasing turbidity levels up to 40 ml (treatment C levels), above which they would decline (Fig. 4).

3.1.4. Atrina condition

$CI_{flesh:length}$ shows a negative but non-significant relationship with increasing volume of sediment added ($R=0.40$; Fig. 5a). There was no significant difference in $CI_{flesh:length}$ of *Atrina* from the 'no sediment' treatment compared to those collected at the beginning of the experiment ($P>0.1$, *t*-test with equal variances). *Atrina* from the 'no sediment' treatment had significantly higher $CI_{flesh:length}$ than those from the 3-day treatment ($P=0.08$, *t*-test with equal variances).

Biochemical condition ($CI_{glycogen:length}$) of *Atrina* showed a strongly inverse relationship with volume of sediment added ($R=0.72$; Fig. 5b). There was no significant

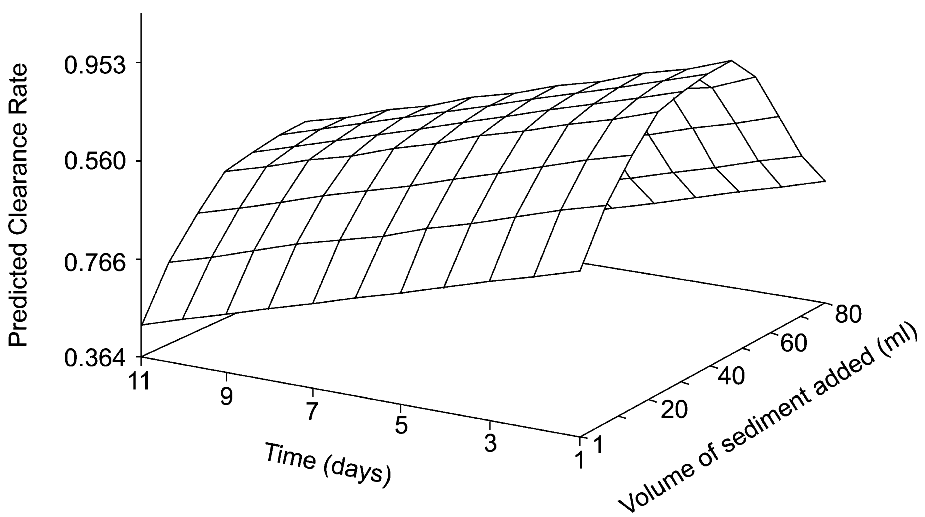

Fig. 4. Predicted response surface relating the effects of treatment (volume of sediment added) and time on *Atrina* clearance rate. Predicted clearance rate = % cleared by two individuals per hour. Twenty six percent of the variability of the data is explained.

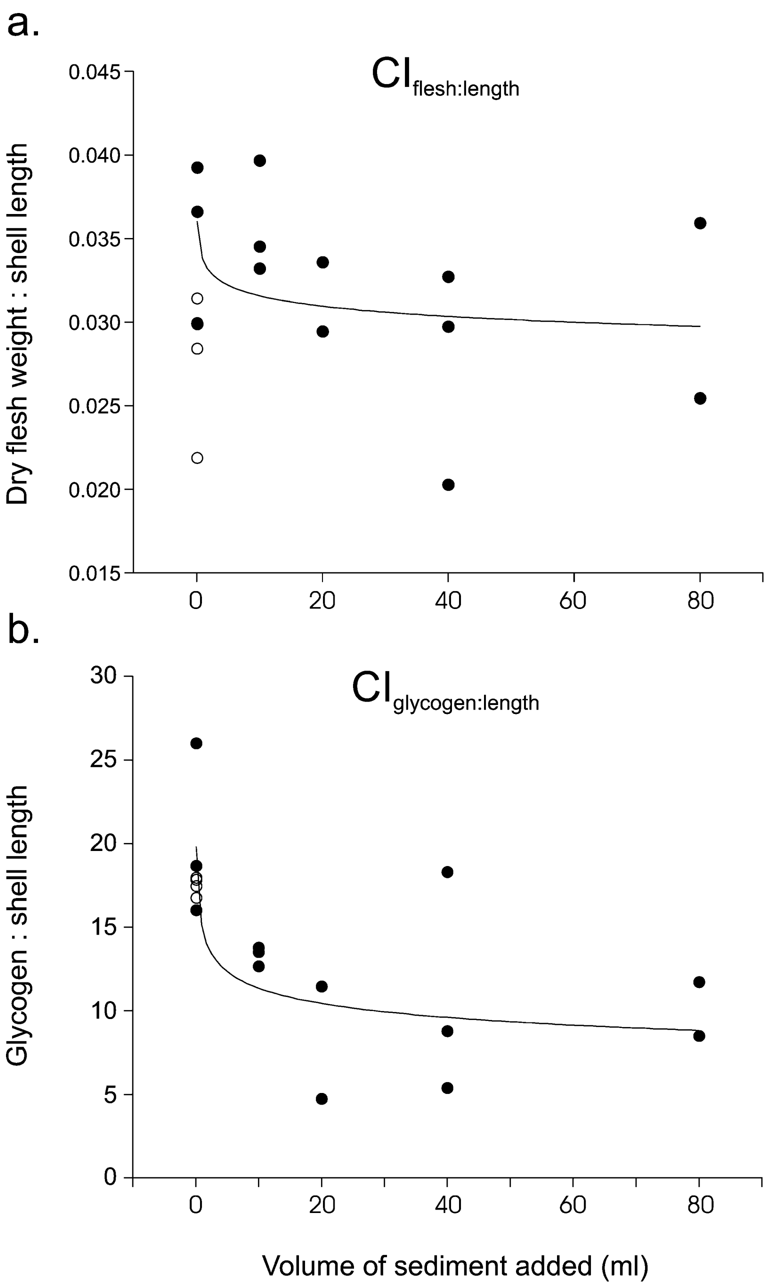

Fig. 5. Regression of volume of sediment added vs. (a) $CI_{flesh:length}$ and (b) $CI_{glycogen:length}$ of *Atrina* at the end of the experiment. The condition of *Atrina* when initially collected is also shown (unfilled circles).

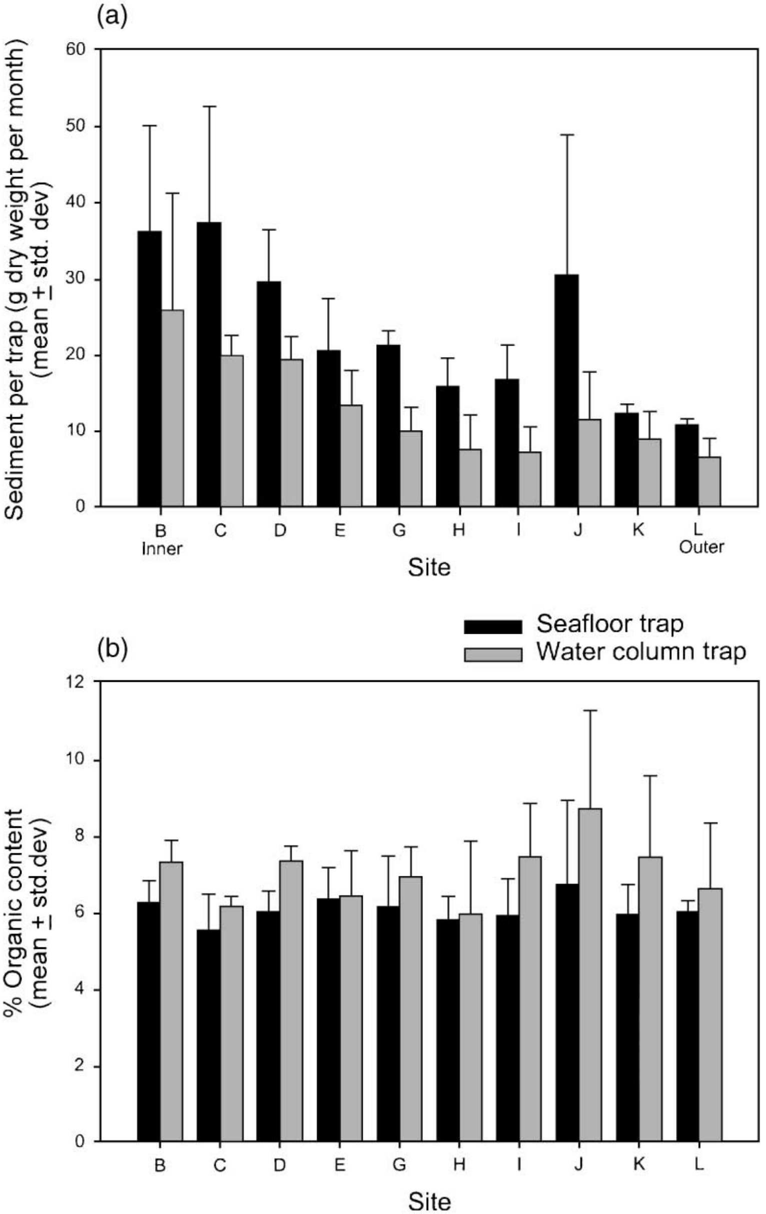

Fig. 6. (a) Dry weight of sediment collected in each seafloor and water column trap at each site per month in the field survey. (b) Percentage of organic carbon of sediment collected in each seafloor and water column trap at each site in the field survey over the 3-month sampling period.

difference in $CI_{glycogen:length}$ of *Atrina* from the 'no sediment' treatment compared to those collected at the beginning of the experiment ($P > 0.1$, *t*-test with equal variances). *Atrina* from the 'no sediment' treatment had significantly higher $CI_{glycogen:length}$ than those from the 3-day treatment ($P = 0.0472$, *t*-test with equal variances).

3.2. Field survey

3.2.1. Sediment

The amount of sediment collected in the traps per month showed a general increase with distance from the mouth of the estuary (Fig. 6a). Site J did not follow the trend due to anomalously high amounts of sediment collected during the third month (i.e., between 11th March and 7th April). More sediment was collected in the seafloor traps than in the water column traps, however the relative proportion of sediment caught in the two trap types was similar between sites. For both trap types we observed an approximately twofold difference in the amount of sediment collected between the innermost and outer estuary sites (i.e., compare sites B and C with sites K and L). Despite the observed trends

Table 3
Median particle size and % of particles 2–12 μm in size of sediment collected in the seafloor and water column traps during the field survey

Site	Water traps, Median particle size	Seafloor traps, Median particle size
B	3.23 (± 0.40)	3.77 (± 0.21)
C	3.10 (± 0.14)	3.40 (± 0.14)
D	3.70 (± 0.26)	3.77 (± 0.23)
E	3.56 (± 0.23)	3.77 (± 0.25)
G	3.77 (± 0.25)	3.57 (± 0.21)
H	3.70 (± 0.17)	3.57 (± 0.12)
I	3.37 (± 0.51)	3.40 (± 0.10)
J	3.45 (± 0.07)	3.50 (± 0.00)
K	3.53 (± 0.15)	3.73 (± 0.25)
L	3.63 (± 0.12)	3.70 (± 0.17)
Site	**Water traps, % Particles 2–12 μm**	**Seafloor traps, % Particles 2–12 μm**
B	94.33 (± 4.04)	93.33 (± 1.15)
C	96.00 (± 2.83)	94.50 (± 3.54)
D	95.00 (± 1.73)	94.33 (± 1.53)
E	93.33 (± 3.21)	95.33 (± 1.15)
G	92.00 (± 1.73)	92.67 (± 1.53)
H	95.00 (± 1.00)	93.66 (± 1.15)
I	92.33 (± 0.58)	92.67 (± 1.15)
J	95.00 (± 4.24)	96.50 (± 2.12)
K	95.33 (± 1.53)	94.67 (± 2.52)
L	92.00 (± 1.73)	93.33 (± 2.52)

Values given are mean ± standard deviation per month.

down the estuary in the quantity of sediment collected, there were no patterns in the amount of settling organic matter (Fig. 6b). The median particle size of sediments collected in the traps averaged from 3.1–3.7 μm (Table 3) and was consistent over the 3 months. Most relevant to effects of sediment on the condition of *Atrina* is the proportion of sediment in the particle size range that is accessible to the bivalves (i.e., able to be processed). Generally, particles 2–12 μm in size are utilised by bivalves (Jorgensen, 1990). At all sites at least 92% of the particles collected in both trap types were within this size range (Table 3).

3.2.2. Atrina condition

Both the physical and biochemical condition were lowest in the *Atrina* from the innermost estuary sites. These sites also had the highest amounts of sediment collected in the water column traps (Fig. 6a). Both condition indices reveal a significant negative relationship with increasing sediment settling flux (Fig. 7a). In this graph we have compared *Atrina* condition with the average amount of sediment collected in the water column traps (50 cm above the seafloor) per month. There were no statistically significant differences in shell length of *Atrina* between sites ($R = 0.12$), with a range from 17.3 to 27.0 cm across all sites.

Atrina are likely to expend more energy processing large amounts of sediment particles, hence increased suspended sediment may have a negative effect on condition. However, increased food quantity or quality could offset or alter this negative relationship. Hence, the effect of increased organic content on *Atrina* condition was also investigated. There was a weak, positive (but non-significant) relationship between *Atrina* condition and percent organic content of the sediment collected in the water column traps per month (Fig. 7b).

3.3. Transplant experiment

3.3.1. Sediment

The same general patterns in suspended sediment flux noted in the field survey were apparent in the transplant experiment. The amount of sediment collected in the water column traps each month showed a general increase with distance away from the mouth of the estuary (Fig. 8a). Traps at the innermost site (Site A) collected the highest amount of sediment. There was a large difference between the amount of sediment collected at this site (108.09 g dry weight per month) and the outermost site (Site L; 23.39 g dry weight per month) (Fig. 8a).

The high levels of sediment also corresponded with increased amounts of settling organic matter (Fig. 8b). This contrasts with results of the survey (conducted from January to April 1998) where the amount of settling organic matter did not differ with site (Fig. 6b). However, the ranges of organic levels differed between the survey and transplant experiment, perhaps accounting for the difference in trends. In the transplant experiment (conducted from July to October 1998), the organic contents ranged from 1.14% to 6.63% while those measured in the survey were higher (5.93% to 8.68%). The median particle size of sediments collected in the traps over the 3-month transplant experiment was very consistent between sites, and ranged from 1.73 to 2.02 μm (Table 4). Site A had the

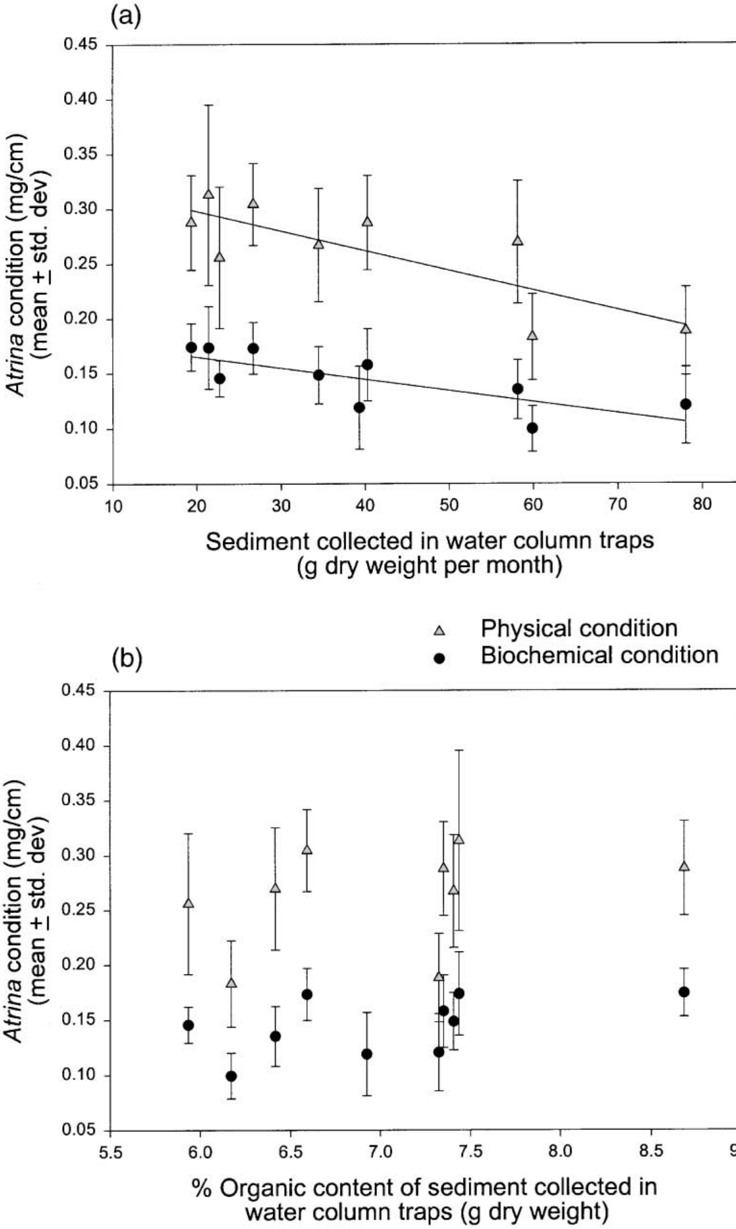

Fig. 7. (a) Relationship between *Atrina* condition and the amount of sediment collected in the water column traps per month in the field survey. Physical condition ($CI_{flesh:length}$): y (mg/cm) = 3.34 (mg/cm) – 0.02 ((mg/cm)/g)x, $R = 0.80$, $P = 0.0100$. Biochemical condition ($CI_{polymeric:length}$): y (mg/cm) = 1.86 (mg/cm) – 0.01 ((mg/cm)/g)x, $R = 0.77$, $P = 0.0090$. (b) Relationship between *Atrina* condition and the % organic content of sediment collected in water column traps in the field survey. Physical condition: $R = 0.33$, $P = 0.3900$. Biochemical condition: $R = 0.52$, $P = 0.1090$.

greatest variance (Table 4). Table 4 illustrates that, for all sites, 99.81% or greater of the particles collected were within the appropriate size range available to suspension feeding bivalves.

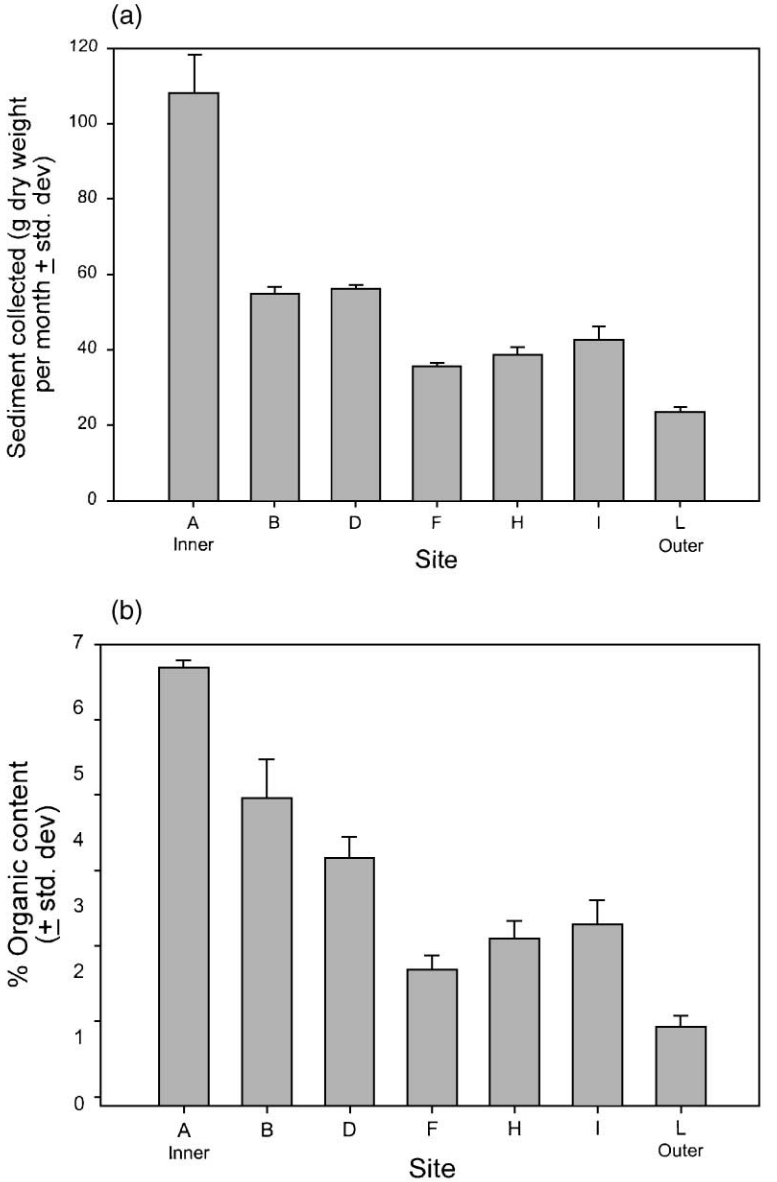

Fig. 8. (a) Dry weight of sediment collected in the water column trap at each site per month in the transplant experiment. (b) Percentage organic content of sediment collected in the sediment traps at each site in the transplant experiment over the 3-month sampling period.

Table 4
Median particle size and % of particles 2–12 μm of sediment collected in the water column traps during the transplant experiment

Site	Median particle size	% Particles 2–12 μm
A	2.02 (± 0.90)	99.85 (± 0.04)
B	1.89 (± 0.26)	99.87 (± 0.02)
D	1.75 (± 0.32)	99.81 (± 0.07)
F	1.80 (± 0.44)	99.81 (± 0.01)
H	1.75 (± 0.17)	99.87 (± 0.03)
I	1.80 (± 0.35)	99.86 (± 0.04)
L	1.73 (± 0.29)	99.82 (± 0.03)

Values given are mean ± standard deviation per month.

3.3.2. Atrina condition

Increased sediment settling flux had a significant negative effect on the physical condition of transplanted *Atrina* ($R = 0.92$, Fig. 9a). The physical condition of ambient *Atrina* at Site L (the collection site) at the beginning of the experiment (July 1998) was 3.08 ± 0.62 mg/cm. *Atrina* at the outer sites gained tissue biomass over the 3-month experimental period, while at the inner sites (with higher sediment settling fluxes) *Atrina* biomass decreased. At the inner most site (Site A), where the dry weight of sediment recorded in sediment traps was greatest, the transplanted *Atrina* had the worst condition. Biochemical condition ($CI_{polymeric:length}$) followed the same pattern as physical condition; i.e., lower condition with increased sediment. The shell length of *Atrina* at the end of the experiment ranged from 18.5 to 28.2 cm across all sites with no statistically significant differences between sites ($R = 0.1312$) (Fig. 10). There were no differences in the range of shell lengths recorded down the estuary indicating that decreases in condition were due to a change in biomass rather than decreases in shell growth rates at the upper sites over the transplant period.

A negative relationship between *Atrina* condition and percent organic content of sediment collected in the sediment traps per month was also found ($R = 0.9110$, Fig. 9b). Hence, even though % organic content was elevated at Site A, it appears that there were no positive effects of the increased quantity of food on *Atrina* condition. This differed from the survey where the relationship was slightly positive, but non-significant (Fig. 7B).

3.4. Comparing survey and transplant measurements

Fig. 11 compares the relationship between the sediment settling flux and *Atrina* condition for both the survey and transplant experiment. The regression slopes for the physical condition of *Atrina* in the survey and the transplant experiment are very similar, despite the fact that they were conducted at different times of the year. This suggests that the relationship between *Atrina* condition and sediment settling flux is consistent in different seasons. It also indicates that the response observed in the survey was in fact due to differences in sediment settling flux around the estuary, rather than population differences in *Atrina*. The survey *Atrina* were collected in April 1998, while those from the

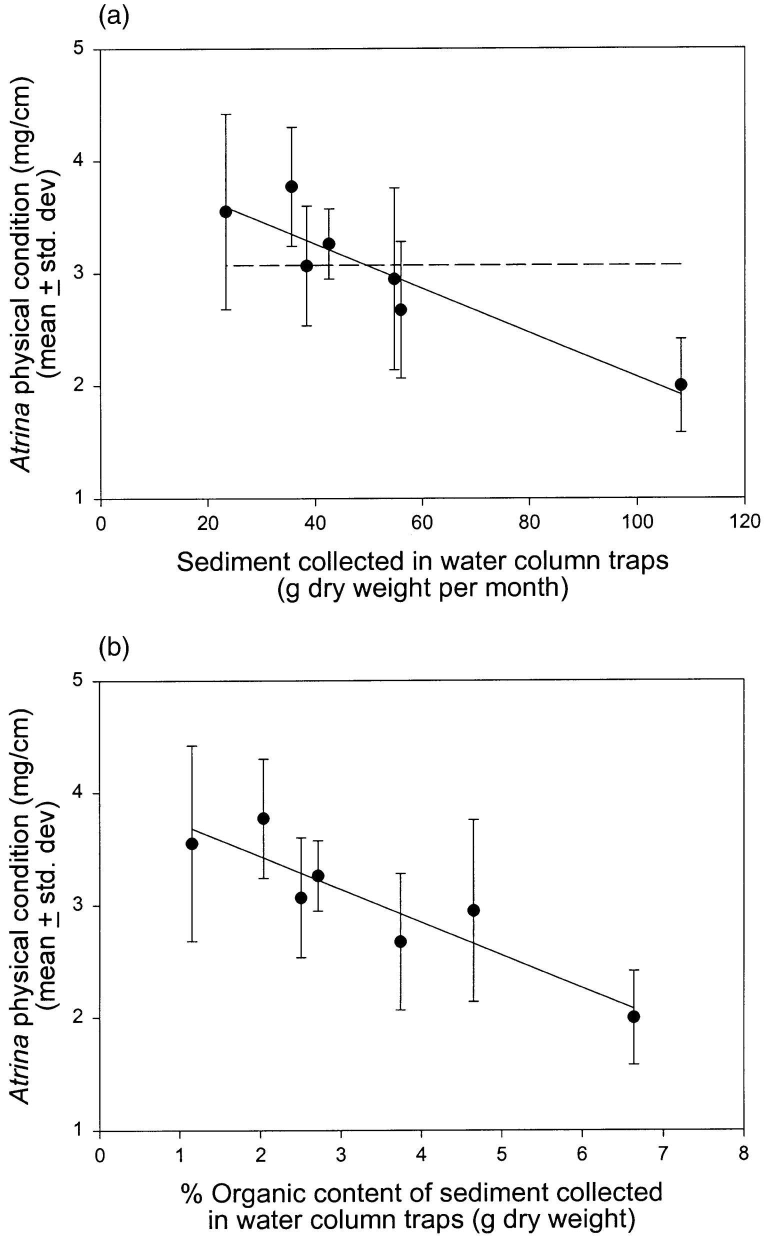

Fig. 9. (a) Relationship between *Atrina* condition and the amount of sediment collected in the water column traps per month in the transplant experiment. Physical condition: y (mg/cm) = 4.06 (mg/cm) − 0.02 ((mg/cm)/g)x, R = 0.92. The dotted line represents the physical condition of transplanted *Atrina* at the beginning of the experiment. (b) Relationship between *Atrina* physical condition and the organic content of sediment collected in water column traps in the transplant experiment. Physical condition y = 4.02 (mg/cm) − 0.88 ((mg/cm)/g)x, R = 0.91.

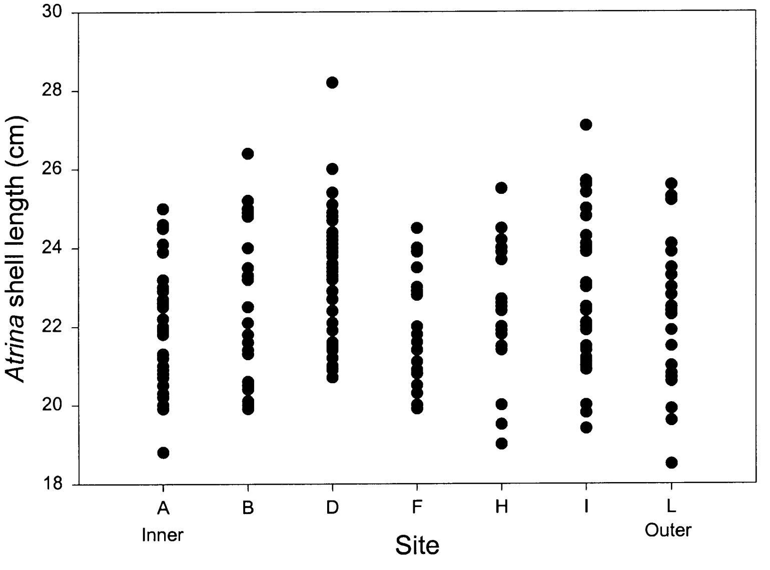

Fig. 10. Relationship between *Atrina* shell length and site for the transplant experiment. $R = 0.13$.

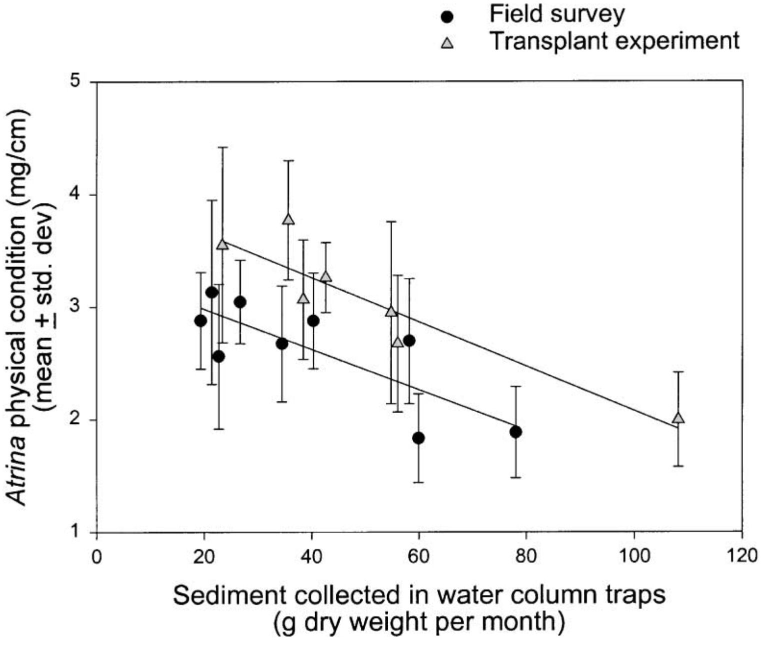

Fig. 11. Relationship between *Atrina* physical condition and the amount of sediment collected in the water column traps per month in the field survey and the transplant experiment. Condition survey: y (mg/cm) = 3.34 (mg/cm) − 0.02 ((mg/cm)/g)x, $R = 0.79$. Condition transplant experiment: y (mg/cm) = 4.05 (mg/cm) − 0.02 ((mg/cm)/g)x, $R = 0.92$.

transplant experiment were collected at the end of October 1998, after a period when reserves of glycogen are being accumulated immediately prior to *Atrina* spawning (authors unpublished data). Hence, the higher physical condition of *Atrina* from the transplant experiment (Fig. 11) would be expected.

4. Discussion

This study has investigated the effect of suspended sediments on the physiological condition of a suspension feeding bivalve. We used a short-term (11-day) laboratory experiment to manipulate suspended sediment, and expose *Atrina* to a range of concentrations naturally recorded in field situations. We then used a field survey of *Atrina* condition along a natural gradient of increasing suspended sediment concentration to validate these results. Finally we experimentally transplanted *Atrina* along this gradient to assess whether any patterns were due to suspended sediment concentration rather than local population differences. Our results clearly demonstrate a negative relationship between suspended sediment concentration and *Atrina* condition. The laboratory experiment has indicated that suspended sediment levels as low as 80 mg/l have adverse effects on *Atrina* condition. The physiological condition of *Atrina* declined in all sediment addition treatments and clearance rates declined above 'threshold' levels of suspended sediment. A consistent negative relationship of increased sediment settling flux on *Atrina* condition was also demonstrated for both the survey and transplant experiment. The survey and transplant experiment determined critical levels of suspended sediment fluxes that result in the loss of condition (49 g dry weight per month) and levels that are so high as to limit the distribution of *Atrina* in field conditions (108 g dry weight per month).

The laboratory study indicated that *Atrina*'s clearance rates increased with increasing suspended sediment concentration (turbidity) to around 120 FTU (turbidity of the 40 ml sediment addition, treatment C), above which they declined (Fig. 4), suggesting that *Atrina* cannot cope with higher suspended sediment concentrations. The treatments with the highest suspended sediment loads generally exhibited the lowest clearance rates (Fig. 4). Clearance rates of several other suspension feeding bivalve species have been tested at suspended seston concentrations ranging from 0 to 570 mg/l, and strong inverse relationships with increasing seston concentrations were found for many of the species studied (e.g., Widdows et al., 1979; Bricelji and Malouf, 1984; Navarro et al., 1992; Navarro and Widdows, 1997). As in our laboratory experiment, clearance rates generally increased up to a 'threshold' concentration, above which they decreased (e.g., Kiorbe et al., 1980; Mohlenberg and Kiorboe, 1981). These threshold concentrations vary depending on the bivalve species (e.g., Hawkins et al., 1999).

Resuspension of bottom sediments has considerable influence on suspended seston concentration and, consequently, concentrations are often much higher in near-bottom compared to surface waters. Benthic suspension feeders in estuaries can experience seston concentrations up to 500 mg/l during resuspension events (Navarro and Widdows, 1997) and levels as high as 1000 mg/l have been recorded in the Tagus Estuary in Portugal (Vale and Sundby, 1987). In New Zealand, suspended sediment concentrations in surface waters of the Marlborough Sounds were estimated at 1000 mg/l as a result of runoff from forestry roads during storms (Fahey and Coker, 1992), suggesting that bottom seston concentrations may exceed these levels. During storm events, the annual sediment load to an estuary may be delivered over a period of days (e.g., Dyer, 1986; Vale and Sundby, 1987; Fahey and Coker, 1992). *Atrina* from the laboratory experiment treatment designed to reflect a large storm event (i.e., 3-day) showed a decline in both biochemical and physical condition compared to *Atrina* from the no-sediment treatment. This was despite the fact that sediment was not added to this treatment for the last 8 days of the experiment, and indicates that even very short-term exposure to elevated suspended sediment concentrations can potentially effect the health of suspension feeding animals.

Mahurangi Estuary is susceptible to the impacts of soil erosion due to its catchment morphology and landuse with high rates of sedimentation delivered to the estuary during flood events. The vast majority ($\geq 95\%$) of suspended sediment throughout the lower Mahurangi Estuary (i.e., south of Grants Island) was in the particle size range utilised by suspension feeding bivalves (i.e., 2–12 μm). This is typical of a turbid estuary, where 70–80% of the particles are in this size range (Widdows et al., 1998). In the transplant experiment, *Atrina* at sites closer to the mouth of the estuary, where suspended sediment fluxes were low, showed increases in physical condition over the 3-month experiment, i.e., the flesh weight increased relative to shell length. However, at the upper estuary sites, where suspended sediment fluxes were high, the transplanted *Atrina* lost condition. The fact that no natural *Atrina* beds were present at this site suggests this level of suspended sediment (i.e., 108 g dry weight per month) may be so high that longer-term survival is inhibited. Even at intermediate sediment fluxes (i.e., 49 g dry weight per month) the physical condition or biomass of *Atrina* decreased relative to their original condition. High suspended sediment loads decrease feeding efficiency resulting in decreased food uptake and increased energy expended in the production of pseudofeces. A loss of utilisable energy sources such as protein and sugars results in decreased energy available for reproduction and growth and at certain levels will ultimately result in death. This study has determined critical levels of suspended sediments that result in the loss of biomass and levels that are so high as to limit the distribution of *Atrina* in field conditions. This relationship was consistent between the transplant experiment that integrated ecological effects over short monthly time scales, and the survey which reflected longer time scale effects. Therefore, we have provided empirical evidence of negative effects of suspended sediment on *Atrina* condition rather than effects due to local population differences, or other environmental gradients within the estuary.

Our findings are consistent with those of other field studies that have investigated effects of sedimentation on benthic communities. For example, gradual sedimentation of Kane'ohe Bay (Hawaii) resulted in the loss of suspension feeding populations and a macrobenthic community with low diversity, small mean body size, low biomass, and relatively low productivity (Smith and Kukert, 1996). Peterson (1985) also documented macrofaunal changes following an intense rainstorm that caused catastrophic sedimentation. Deposition of silt and clays substantiality increased mortality of suspension feeding bivalves, with higher mortality among infaunal, siphonate suspension feeders than among infaunal siphonate deposit feeders.

The loss of key suspension feeders at high concentrations of suspended sediments might induce large-scale alteration of energy flow in the community (Loo and Rosenberg, 1989; Pearson and Rosenberg, 1992; Norkko and Bonsdorff, 1996). *Atrina* adds complexity to soft sediment habitats by modifying boundary flow conditions, providing predation refuges, and substrates for epifaunal settlement and has a strong influence on local macrobenthic community composition (Cummings et al., 2001). Hence, with large scale disturbed areas effects on macrobenthic community composition and food web complexity would be expected. In addition, *Atrina* filter large volumes of particulate matter from the water column and act to stabilise the bed. At high densities, the feeding activity of suspension feeders can alter the quality and quantity of seston in the water column (Dame et al., 1980), and can also significantly influence phytoplankton population dynamics (Cloern, 1982; Peterson and Black, 1987). Hence, a loss of *Atrina* would also be expected to affect clearing of sediment from the water column, and the seston food supply, and to increase resuspension from the seabed under high flow conditions. A further consideration is that at suspended levels where organisms are sublethally stressed, the role of multiple stressors can become more important (e.g., Peterson and Black, 1988). The potential effect of the loss of *Atrina* as well as the role of multiple stressors requires further investigation.

Increases in catchment runoff, elevated sedimentation and water column turbidity are symptoms of coastal development. Such changes lead to alterations in community structure, with strong declines in abundance of sensitive species and increased dominance of opportunistic species (Saiz-Salina and Urkiaga-Alberdi, 1999). Changes in sediment regimes where coastal systems experience continuous inputs of sediment result in functional and structural changes in soft sediment benthic communities over broad scales. However, few studies have been able to document such broad scale changes due to the spatial extent of potential impacts and the lack of long-term monitoring data and relevant control sites (Ellis et al., 2000). This study has demonstrated that *Atrina* distribution can be limited by suspended sediments and illustrates the potential for the loss of a key suspension feeding species in areas of high sedimentation. Given that *Atrina* have a strong influence on the structure and diversity of benthic communities, we expect that this could have serious, large-scale effects on estuarine ecosystems in areas of high suspended sediments.

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