Benthic nutrient fluxes along an estuarine gradient: influence of the pinnid bivalve *Atrina zelandica* in summer

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ABSTRACT: Benthic nutrient fluxes (BNF) can supply 30 to 100% of the nutrient requirements of benthic and pelagic algae in an estuary, and can, thus, potentially sustain benthic and pelagic primary production within the estuarine food web. While BNF can be influenced by microbial processes, epibenthic suspension-feeding bivalves have the potential to alter fluxes by their influence on the community composition of surrounding macrofauna and benthic boundary conditions, and their feeding activities. In Mahurangi Harbour, New Zealand, the large suspension feeding pinnid *Atrina zelandica* (hereafter referred to as *Atrina*) occupies large areas of the harbour floor. Consequently, *Atrina* have the potential to substantially influence the BNF and, thus, primary production, and the food supply to the filter feeding community within the harbour, including the rack-farmed Pacific oyster aquaculture industry. Mahurangi Harbour is almost always isohaline, but exhibits a strong gradient in suspended sediment concentration, which declines from head to mouth. As *Atrina* increase their rate of pseudofaeces production with increases in suspended sediment concentration, we conducted *in situ* light and dark paired benthic chamber experiments with and without *Atrina* at 4 stations along this turbidity gradient, to determine their effect on BNF. Our results showed substantially greater BNF from *Atrina* beds than bare sediments. We also found greater net BNF (difference between *Atrina* beds and bare sediment) in the less turbid water under dark conditions, but enhanced water column nutrient supply in the more turbid water in light, due to *Atrina* excretion of ammoniacal nitrogen (NH_4-N). On an areal basis, we estimate that BNF from *Atrina* beds may account for up to 80% of the nutrient supply for pelagic primary production and, thus, they are of major importance to the sustainability of aquaculture in this harbour.

KEY WORDS: Benthic nutrient flux · Benthic chambers · Estuarine turbidity gradient · *Atrina zelandica* · Microphytobenthos

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INTRODUCTION

Benthic nutrient fluxes (BNF) can supply a substantial proportion of the nutrient requirements of benthic and pelagic algae in an estuary (30 to 100%) and, thus, they potentially sustain the benthic and pelagic primary production within the estuarine food web (Kemp & Boynton 1992, Berelson et al. 1998, Gibbs et al. 2002, Sundbäck et al. 2003). Generally, investigations of BNF concentrate on the role of microbial processes, associ-ated with coupled nitrification–denitrification, and the microphytobenthos, which intercept the nutrient fluxes at the sediment–water interface (e.g. Sundbäck et al. 2000, 2004). Microphytobenthos may fully utilise nutri-ents for growth in daylight (MacIntyre et al. 1996, Webster et al. 2002, Sundbäck et al. 2004), fix nitrogen (Newell et al. 2002), and increase the cohesiveness of the sediments, thereby reducing resuspension (Del-gado et al. 1991, Stal 1994, Miller et al. 1996). How-ever, the presence of benthic animals can also be an

important part of the nutrient dynamics of an estuary (e.g. Newell et al. 2002).

Bioturbation and grazing pressure by macrofauna can destabilise the sediments (de Deckere et al. 2001), stimulating microbial activity and enhancing denitrification (Gilbert et al. 1998). However, the presence of large benthic animals may also stabilise the sediments, and affect the composition and functioning of macrofaunal communities (Cummings et al. 1998, 2001, Ellis et al. 2000, Norkko et al. 2001, Hewitt et al. 2002, Reise 2002). Abundant suspension-feeders may build loose hummocks, multi-species epibenthic thickets or solid reefs, accommodating diverse epibenthic assemblages. Their raised and rough surfaces alter benthic boundary conditions (Green et al. 1998) and, hence, turbulence (Reise 2002), while their biodeposits may enrich the sediments and smother the microphytobenthos. Below the sediment surface, tubes and burrows of sessile or discretely motile animals provide microoxic zones (Munksby et al. 2002) where biogeochemical transformations may impact on the BNF (Boynton et al. 1982, Dame & Libes 1993, Gilbert et al. 1997, 1998, Herman et al. 2000, Sundbäck & Miles 2000).

In estuaries, strong gradients of salinity, turbidity, nutrients, and light can all influence primary production (Malone et al. 1988, Gallegos et al. 1992, Gibbs & Vant 1997). Suspended sediment may be particularly important, influencing turbidity and light, and the feeding efficiency and biodeposit production of suspension feeders (Barillé et al. 1997, Hawkins et al. 1999). Suspended sediment loads may also determine the distributional limits of benthic macrofaunal suspension-feeders within the estuary (Quijón et al. 1996, Ellis et al. 2002). At Mahurangi, a small, 25 km² harbour on the eastern shores of the North Island of New Zealand, populations of the largest benthic organism, the horse mussel *Atrina zelandica* Gray (hereafter referred to as *Atrina*) appear to be declining (authors' unpubl. data). *Atrina* are large (up to 30 cm long) suspension-feeding pinnid bivalves common in sandy and muddy soft-sediment subtidal environs around NE New Zealand (Powell 1979, Cummings et al. 1998). *Atrina* protrude above the sediment surface (commonly 7 cm) and often form large patches of up to 100 m⁻² (Hewitt et al. 2002) on the seafloor, adding to the complexity of the soft-sediment habitat by providing predation refuges and substrate for epifaunal attachment. *Atrina* have been found to increase their rate of biodeposit (pseudofaeces) production as sus-
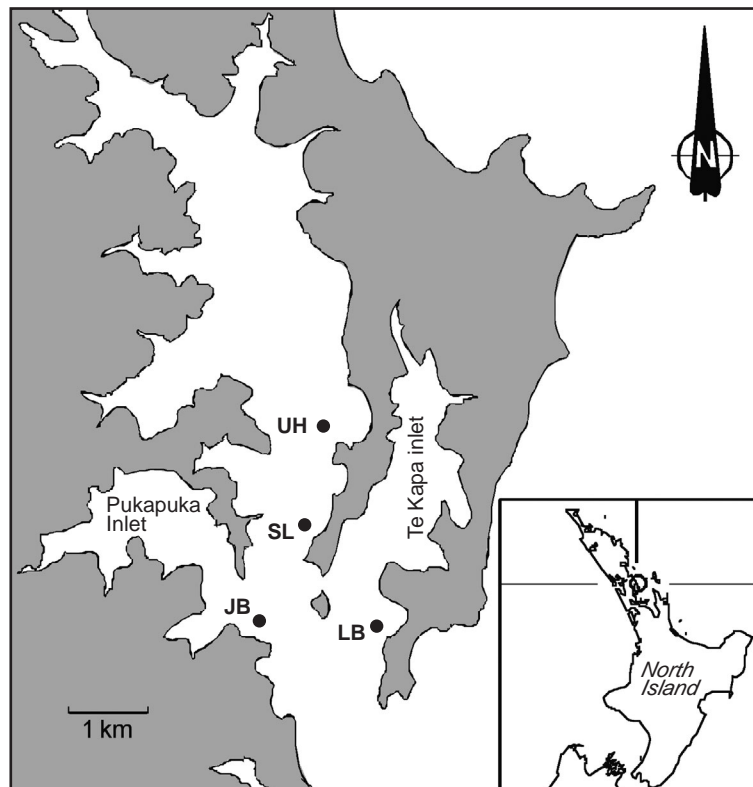

Fig. 1. Map of Mahurangi Harbour showing the location of the 4 study sites. Sites are approximately 1.5 km apart and have a 4 to 8 m water depth (high tide)

pended sediment concentrations increase (Norkko et al. 2001, Ellis et al. 2002), which in turn may cause enhanced burial of microphytobenthos and changes in the BNF. Consequently, the decline in *Atrina* populations may have a major impact on the nutrient dynamics and productivity of this harbour.

We test this hypothesis by examining the spatial differences in benthic biomass, and nutrient and dissolved oxygen fluxes across the sediment–water interface *in situ*, with and without *Atrina*, along the turbidity gradient in Mahurangi Harbour. We also use natural abundance stable isotope signatures to establish links between the *Atrina* and the sediments in which they live.

MATERIALS AND METHODS

Study site. Mahurangi Harbour is a small (25 km²), shallow but deeply incised estuary in NE New Zealand (Fig. 1), extensively used for the rack culture of Pacific oysters *Crassostrea gigas* in the intertidal zone. As the main freshwater input is a relatively small stream (mean annual flow ca. 0.25 m³ s⁻¹), the harbour is almost always isohaline (salinity > 33). However, there

is a strong turbidity gradient down the estuary. Four sites ca. 1.5 km apart were selected along the turbidity gradient on the main axis of Mahurangi Harbour (Fig. 1): Site UH, near the inner harbour limit of natural *Atrina* beds; Site LB, near the mouth of the harbour; and Sites SL and JB distributed between these other 2 sites. The sediments at these sites have previously been characterised (Ellis et al. 2002) as fine sandy silt at UH (56.39 µm) and LB (61 µm), and fine to medium sandy silt at SL and JB (105.50 µm). Water depth at Sites UH, JB, and LB was around 4 to 5 m but around 8 to 9 m at SL, where there appeared to be bed scouring. Water flow within Mahurangi Harbour is driven mainly by the semi-diurnal tides, with maximum velocities of 0.3 and 0.7 m s^{-1} at peak neap and spring tides, respectively.

Three sites (SL, JB, and LB) were studied on 24 January 2001 (summer, Southern Hemisphere), and a more detailed study at all 4 sites was made on 6 February 2002. Both studies were conducted under bright sunny conditions, after an extended period without rain (Fig. 2A).

Atrina **respiration and excretion.** In January 2001, to quantify respiration and excretion rates, several *Atrina* of similar size (205 to 230 mm length) were collected from each of 3 sites (Sites SL, JB, and LB). Their shells were cleaned of epibenthos and they were conditioned in mesh bags at the same site overnight. On the following morning, the *Atrina* were retrieved and transported to the shore base in a troughs of aerated ambient seawater pending estimation of respiration and excretion rates. Individual *Atrina* were incubated in a 2.6 l water-filled, opaque, stirred chamber, which was then sealed and submerged in a controlled temperature water-bath for 1 h. Initial and final water samples were taken for analysis of dissolved oxygen (DO) and ammoniacal nitrogen (NH$_4$-N). *Atrina* were initially incubated in water collected from the same site from which they were collected. Later, the *Atrina* from each site were incubated in high turbidity water from the inner harbour (Site UH). Three replicate measurements were made of each treatment. Controls were run concurrently without an *Atrina* in the chamber.

In situ **incubations.** Incubations were made in sets of 4 treatments, <4 m apart, at each site: light and dark with 1 *Atrina* (treated), and light and dark without *Atrina* (controls), using stirred benthic chambers (area 0.25 m^2; volume 0.025 m^3). The 0.5 m square aluminium chamber bases were pressed into the sediments to a depth of 0.15 m by divers the day before incubation to seal any infaunal burrows and allow flushing of any sediment disturbance. Incubations began when divers installed the clear or blackened chamber lids and attached the stirrers. Ambient water samples were incubated with each set of chambers in light and dark bottles (1 l PET; light = clear; dark =
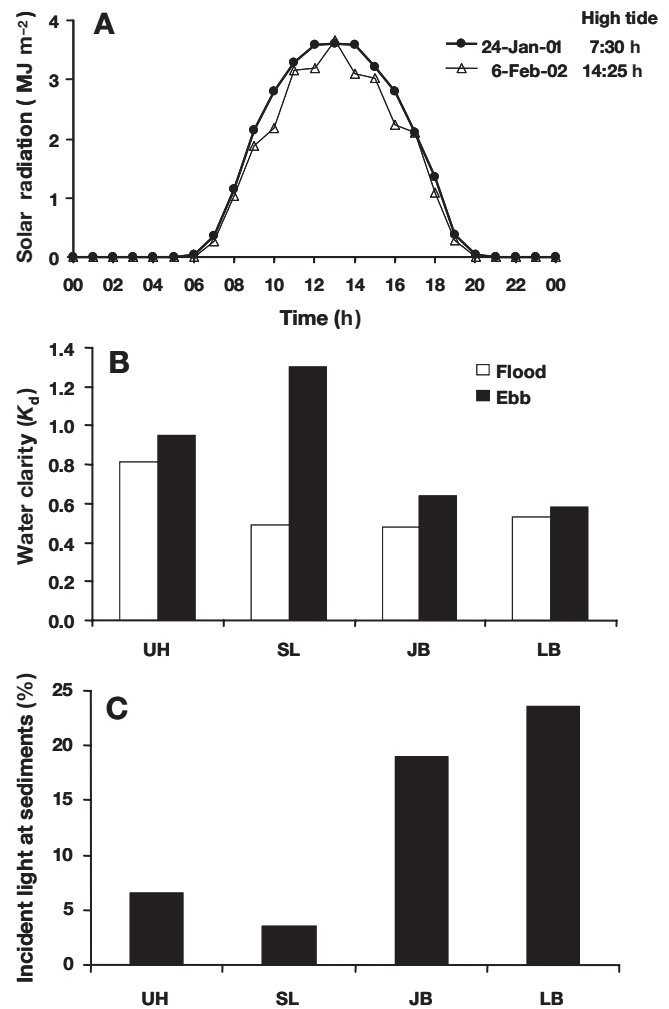

Fig. 2. (A) Solar radiation measured at Warkworth meteorological station at the head of Mahurangi estuary on the 2 sampling dates (NZST). (B) Water clarity (K_d) on the flood and ebb tide at each site. (C) Mean percentage of surface irradiance measured at the chamber depth at each site

wrapped in black tape) without sediment to allow correction for any water column effects. A replicate sample of ambient water was retained for immediate analysis of DO and subsequent nutrient analysis as the initial water sample.

Water samples were drawn from each benthic chamber, at timed intervals over a period of about 5 h, via a 3 mm (inside diameter), hard, flexible, nylon tube to the surface, directly into a sample bottle, under reduced pressure. The initial volume of the tube (7 ml m^{-1}) was discarded before the chamber water was collected. Replacement water into the chamber was supplied from a compensation water bag attached to the chamber via a connecting tube. The compensation water was also sampled and analysed to allow correction for chamber water nutrient dilution during sampling.

Measurements. Profiles of photosynthetically active radiation (PAR) for downward irradiance were obtained using a Li-Cor model 194B cosine-corrected underwater sensor. Direct measurements of the percentage of surface light at the depth of the chambers were made in February 2002, and the attenuation coefficient (K_d) calculated at each site on the flood and ebb tide.

DO concentration was measured in each water sample, including initial samples, immediately upon collection, using a Yellow Springs Instrument (YSI) model 5731 stirred BOD bottle probe. *Atrina* and benthic respiration were measured as oxygen consumption in the dark chambers, and benthic gross primary production (GPP) was calculated from the net increase in oxygen in the light relative to dark chambers (e.g. Welsh et al. 2000). Values for respiration and GPP were corrected for water-column-only effects measured in the light and dark bottles incubated with the chambers at each site. GPP as g carbon (C) m^{-2} d^{-1} was estimated using the oxygen-to-carbon conversion factor of 0.31 g C g^{-1} O_2 (Schramm et al. 1984).

The water samples were filtered under reduced pressure (<20% reduction to avoid cell rupture) through Whatman 2.5 cm GF/C glass fibre filters directly into the sample storage bottle on a portable collecting vacuum manifold. The initial 20 ml of sample was used to rinse the filter and sample bottle, and was discarded. All filtrations were performed onboard the boat on site and completed within 1 h of collection. All water samples were stored on ice pending freezing and returning to the laboratory for analysis. Particular care was taken to ensure that handling procedures did not introduce NH_4-N contamination.

Water and sediment samples for algal species dominance were preserved in Lugol's iodine solution prior to settling in Utermöhl chambers and investigation using an inverted Lietz microscope (Utermöhl 1958).

Where appropriate, filters were retained for chlorophyll *a* determination. Each filter was folded in half (inwards) and stored in an individual polycarbonate envelope (Secol security envelopes, Secol) in a watertight, sealed plastic bag on crushed ice in the dark pending freezing and analysis on return to the laboratory. Chlorophyll filters were analysed by the 90% acetone extraction method of Strickland & Parsons (1972).

Sediment cores (two 2.5 cm diameter, 2 cm deep) from each chamber for chlorophyll determination were extracted from freeze-dried aliquots by boiling in 95% ethanol. The absorbance of the extract at 665 and 750 nm, before and after acidification with hydrochloric acid, was measured in a Shimadzu UV-160A spectrophotometer. Sediment chlorophyll concentration was calculated using the equations of Sartory (1982).

Sediment organic content was determined gravimetrically on a ca. 6 g (wet wt) aliquot which was oven- dried at 98°C for 48 h, weighed, combusted at 550°C for 3 h, and reweighed. Organic content was calculated as the loss on combustion.

One *Atrina* specimen from each site in 2002 was measured and dissected to separate stomach, gonad, and flesh before stable isotope analysis without lipid extraction. All tissue samples were freeze-dried and stored in sealed containers pending analysis.

Freeze-dried sediment and *Atrina* tissue samples for stable isotope determination were weighed into pure tin (Sn) capsules, combusted in a Fisons NR1500 elemental analyser at 1020°C, and carbon and nitrogen isotopic composition measured on a DeltaPlus (Finnigan MATT) continuous flow, isotope ratio mass spectrometer. Stable isotope ratios are reported in standard delta (δ) notation per mil (‰) as: $\delta X = [(R_{sample}/R_{standard}) – 1] \times 10^3$, where X is ^{13}C or ^{15}N and $R = {}^{13}C/{}^{12}C$ or $^{15}N/{}^{14}N$, respectively. Standard reference materials are PDB limestone for carbon (a calibrated working standard of CO_2 gas was used), and air was the standard for nitrogen (a calibrated working standard of N_2 gas was used).

Water samples were analysed for total NH_4-N, nitrate + nitrite nitrogen (NO_3-N), dissolved reactive phosphorus (DRP) and total phosphorus (TP) using the standard methods of Grasshoff et al. (1983) on an AlphKem series 500 air-segmented continuous flow marine auto-analytical system.

Atrina excretion was estimated from the increase in NH_4-N in the incubation chamber water and calculated as a rate in mg h^{-1}. The change in nutrient concentration, and the volume and area of the benthic chambers, were used to calculate the sediment nutrient efflux rates in µmol m^{-2} h^{-1}. These results were corrected for any control bottle changes (water column effects without sediment) and compensation water inputs. These results are regarded as net rates of exchange between sediment and water after denitrification and microphytobenthos uptake of nutrients released from the sediments.

As only 1 *Atrina* was enclosed in each treated chamber and the control chamber was within 4 m of the treated chamber, it is reasonable to assume that differences between the control and treated chambers will be mostly due to the presence of the *Atrina* and its associated infaunal and floral community. Consequently, the differences attributable to the presence of the *Atrina* have been estimated by subtracting the control from the treated chamber results. These have been compared with the *Atrina* respiration and excretion results.

Statistics. Paired *t*-tests were conducted to determine whether the effect of *Atrina* was consistent between sites and dates. However, it was anticipated that

changes occurring along the turbidity gradient were a result of changes to *Atrina* behaviour. Information on the turbidity gradient in the harbour was available from a number of sources: measurements of suspended sediment concentrations made in January 2001, the attenuation coefficient calculated in February 2002 (adjusted to constant depth), and settling flux measurements in traps on a number of occasions from Ellis et al. (2002). Each of these was ranked from high to low and an average rank of turbidity derived for each site.

An analysis of covariance was undertaken to determine whether differences in NO_3-N and NH_4-N fluxes, respiration, and GPP among sites could be predicted by the turbidity gradient, and whether any relationship observed was consistent on the 2 dates (January 2001 and February 2002).

RESULTS

Water column

Water clarity (Fig. 2B) varied over the semi-diurnal tide with generally clearer water on the flood than ebb tides. The difference in clarity between flood and ebb tides was less than the clarity difference between sites at LB and JB than at UH, with K_d values of 0.58 to 0.53, 0.48 to 0.64, and 0.81 to 0.95, respectively. At Site SL, water clarity varied considerably between phases of the tide with K_d values of 0.49 and 1.3 on the flood and ebb tides, respectively. Water clarity on the ebb tide at SL was lower than at the up-gradient site at UH, which is consistent with the observation of apparent bed scour at SL. The very much clearer water at SL than UH on the flood tide suggests that incoming oceanic water entrains or suspends a substantial load of sediment before reaching the UH site. It also indicates that Site SL is at the transition zone of the upper limit of clear water on the flood tide. Although less light reached the sediments at Sites UH and SL than at JB and LB (Fig. 2C), there was sufficient light for photosynthesis by microphytobenthos and phytoplankton at all sites.

Phytoplankton species composition was dominated by small flagellates and the diatom *Chaetocerous* sp. at the outer harbour sites. At the inner harbour sites, small flagellates were dominant. The diatom *Pseudonitzschia seriata* was found at all sites and the diatom *Skeletonema* sp. at the outer

harbour sites only. In the benthos, there were few dinoflagellates. Communities were dominated by diatoms *Gyrosigma* spp. and *Nitzschia* spp., although *Gyrosigma* spp., a resuspendor, was present at low levels only in the 2 inner harbour sites. Phytoplankton biomass, as indicated by chlorophyll *a* concentrations, was highest at Site UH and decreased down the gradient to Site LB (Table 1). Initial and final concentrations in the light bottles incubated with the benthic chambers demonstrated rapid growth with chlorophyll concentrations increasing by 25 to 32% during the 5 h incubation period. There was essentially no growth in the dark bottles, as expected.

Water column chemistry down the estuarine turbidity gradient (Table 1) was essentially constant for DRP and NH_4-N concentrations, while TP concentrations were higher in the inner harbour. This is consistent with the much higher phytoplankton biomass and turbidity at the inner harbour sites.

Atrina

Net respiration and excretion rate estimates for *Atrina* from Sites SL, JB, and LB (Table 2) indicate that, while excretion rates were similar, there was lower respiration for the *Atrina* from Site JB than those from the other 2 sites. When suspended solids concentrations increased, net excretion rates increased dramatically by a similar amount, more than doubling for

Table 1. Water chemistry and chlorophyll *a* concentrations in initial and final 5 h bottle incubations in February 2002 (data in square brackets refer to 2001). All results are expressed in mg m^{-3}. NH_4-N: ammoniacal nitrogen; DRP: dissolved reactive phosphorus; TP: total phosphorus. Nitrate-nitrogen concentrations were below the detection level

| Site | NH_4-N | DRP | TP | Chlorophyll *a* | | |
				Initial	Light + 5 h	Dark + 5 h
UH	9	7	28	2.7	3.6	2.8
SL	11 [6]	8 [7]	23	2.0 [0.6]	2.9	2.0
JB	10 [7]	7 [8]	17	0.9 [0.6]	1.9	1.5
LB	11 [4]	7 [6]	17	0.9 [0.5]	1.1	1.0

Table 2. *Atrina zelandica*. Mean (n = 3), net oxygen (O_2) respiration and ammoniacal nitrogen (NH_4-N) excretion rates (mg h^{-1}) (±SD) from 3 sites incubated in water from the same site (ambient) and Site UH (turbid). Results are corrected for controls. Measurements were made in January 2001

| Site | O_2 respiration | | NH_4-N excretion | |
	Ambient	Turbid	Ambient	Turbid
SL	−3.21 (1.11)	−3.80 (0.81)	0.099 (0.046)	0.219 (0.110)
JB	−1.89 (0.89)	−2.91 (1.15)	0.093 (0.001)	0.216 (0.127)
LB	−3.61 (1.63)	−2.91 (0.98)	0.100 (0.052)	0.224 (0.120)

Atrina from all sites. Respiration results were more variable when suspended solids concentrations increased, with increases for Sites SL and JB, but a decrease for Site LB.

As only 1 *Atrina* was collected from each site in February 2002, measurements are only used as an indication of relative condition at the 4 sites (Table 3). Condition index (dry flesh wt divided by shell length, Ellis et al. 2002) was substantially greater at Site LB than at the other 3 sites. The separation of *Atrina* tissue into stomach, gonad, and other flesh shows a much larger mass of gonad material in the *Atrina* from Site LB, suggesting that the *Atrina* were preparing to spawn.

Elemental and stable isotope values in the sediments, *Atrina* faeces, and *Atrina* flesh (excluding gonad and stomach tissue) (Tables 4 & 5) showed different patterns down the estuarine turbidity gradient. Sediment $\delta^{13}C$ values show little indication of a terrigenous source (expected $\delta^{13}C$ values $\approx$ –25 to –35‰) or influence from pelagic phytoplankton (expected $\delta^{13}C$ values about –22‰), suggesting that the organic component was not recent and the carbon may have been recycled several times. Whereas % C in the sediments tended to decrease down-gradient, the sediment $\delta^{13}C$ values became more enriched down-gradient with substantial ^{13}C enrichment at Site LB, at the confluence of the Te Kapa inlet. This level of ^{13}C enrichment indicates rapid microbial processing in the sediments at that site.

For nitrogen, both the % N and $\delta^{15}N$ values in the sediments decreased down-gradient, with lowest values at Site LB. Although there was no apparent relationship with distance down-gradient associated with the variability in the % C in the *Atrina* flesh, there was a consistent decline in the % N content. Consequently, there was a marked increase in the C:N ratios in the *Atrina* flesh down-gradient (Table 4).

Although there were small differences between sites for the $\delta^{13}C$ values in the *Atrina* flesh (range –19.14 to –20.56‰) with greatest enrichment (–19.14‰) at SL, there was a small but consistent increase in $\delta^{15}N$ enrichment (from 9.57 to 11.21‰) down-gradient. This enrichment pattern suggests increasing levels of microbial processing, including mineralisation and denitrification, down the estuarine gradient. With respect to the *Atrina* faeces, the $\delta^{13}C$ and $\delta^{15}N$ values were depleted below flesh values (0.4 to 2.1 and 3.0 to 4.1‰, respectively), which is comparable with 1 'trophic' level[1]. However, whereas the $\delta^{15}N$ values of the faecal material were comparable with those of the ambient sediments, the $\delta^{13}C$ values of the faecal material were also substantially depleted (3.2 to 6.2‰) relative to the sediments in which the *Atrina* lived. This suggests that the *Atrina* fed on seston drifting down the estuary, as found by Riera & Richard (1996), rather than resuspended from local sediments. At Site LB, the more enriched $\delta^{13}C$ signatures in the sediments and faecal material suggest that the *Atrina* were feeding on locally resuspended material. However, as the $\delta^{13}C$ enrichment of the flesh was not as great as would be expected relative to the sediments on a proportional basis from the other sites, it is possible that

Table 3. *Atrina zelandica*. Morphology and condition. Condition index = whole tissue dry wt divided by shell length

Site	Shell length (mm)	Tissue dry wt (g)				Condition index
		Whole	Stomach	Gonad	Flesh	
UH	236	6.162	0.105	0.480	5.577	0.026
SL	250	5.495	0.049	0.332	5.114	0.022
JB	210	5.928	0.080	0.388	5.460	0.028
LB	213	8.873	0.153	1.088	7.632	0.042

Table 4. *Atrina zelandica*. Faeces, flesh, and sediment carbon (C) and nitrogen (N) content (%), and C:N ratios

Site	Carbon			Nitrogen			C:N ratio		
	Sed.	Faeces	Flesh	Sed.	Faeces	Flesh	Sed.	Faeces	Flesh
UH	1.07	0.67	38.34	0.09	0.06	9.49	11.89	11.17	4.10
SL	0.99	0.74	39.63	0.08	0.08	6.76	13.20	9.87	5.86
JB	0.60	0.95	40.86	0.05	0.08	6.67	11.32	11.88	6.13
LB	0.76	0.60	39.44	0.05	0.07	5.51	16.89	9.23	7.16

Table 5. *Atrina zelandica*. Carbon and nitrogen natural abundance stable isotope composition (‰) of sediment, *Atrina* faeces, and *Atrina* flesh (excluding gonad and stomach tissue)

Site	Carbon ($\delta^{13}C$)			Nitrogen ($\delta^{15}N$)		
	Sediment	Faeces	Flesh	Sediment	Faeces	Flesh
UH	–17.72	–20.94	–20.56	6.91	6.22	9.57
SL	–15.37	–21.15	–19.14	7.35	7.67	10.69
JB	–16.97	–21.46	–19.71	6.43	6.66	10.60
LB	–10.41	–16.62	–19.37	6.30	7.08	11.21

[1]A trophic level in natural stable isotopic abundance is ca. 1‰ for $\delta^{13}C$ and ca. 4‰ for $\delta^{15}N$. It is the level of isotopic fractionation that normally occurs when food passes through 1 transfer process in the food web

the isotopic data reflect a recent change in *Atrina* food source at Site LB.

Sediments

Sediment % organic or seston contents (Table 6) were similar at Sites UH and SL at 3.48 and 3.59%, respectively, but much lower at Sites JB and LB at 2.29 and 2.87%, respectively. The mean % C content of the sediments followed a similar pattern and there was a strong correlation ($p < 0.001$, $r^2 = 0.902$, $n = 8$) between the mean % organic and the mean % C content of the sediments. As the % N content of the sediments also appears to decrease while the C:N ratio increases (Table 4), this suggests that biological processing is increasing down the estuarine gradient.

Sediment chlorophyll *a* concentrations (Table 6) did not follow the pattern of % organics or % C, with highest values being found at Sites UH and JB at 8.53 and 8.38 µg g^{-1} sediment, respectively. Chlorophyll *a* concentrations were lower at LB (6.49 µg g^{-1} sediment) and lowest at Site SL (4.26 µg g^{-1} sediment). The lower chlorophyll *a* values at SL and LB did not correlate with light, LB having the highest percentage of incident surface irradiance at the sediment surface (23.5%) and SL the lowest (ca. 3.5%). Whereas bed scouring may account for the low light levels at Site SL, scouring seems less likely at Site LB, although it is possible. These data suggest that there is higher grazing pressure at Site LB than the other 3 sites.

The treated minus control chamber data for the light incubations show a consistent pattern of less algal biomass in the treated than control chamber sediments (Fig. 3). This may indicate filtration by *Atrina* and subsequent burial by faeces and pseudofaeces and/or higher grazing pressure by the infauna attracted to the habitat created by *Atrina*. There was also a spatial distribution of less algal biomass in the inner than outer harbour *Atrina* beds. As *Atrina* pseudofaeces production rates are substantially greater in the more turbid inner than clearer outer harbour, this suggests that the burial of the microphytobenthos may be an important process.

Benthic fluxes

Estimates of benthic respiration, benthic gross primary production (GPP), and BNF are made from the oxygen and nutrient data collected in February 2002 and, where possible, compared with similar data collected in January 2001.

Table 6. Sediment chemistry and benthic biomass (chlorophyll *a* content, Chl) and percentage of incident surface irradiance (Irr) reaching the sediments at the depth of the chambers at the 4 sites. Average rank of turbidity was derived for each site from light attenuation coefficients and settling flux data from concurrent field studies (see 'Materials and methods'). Values are means (±SD) of all data (n = 8), except for light (n = 2)

Site	Sediment composition (%)			Chl (µg g^{-1})	Irr (%)	Depth (m)	Turbidity rank
	Organic	C	N				
UH	3.48 (0.28)	1.07 (0.06)	0.09 (0.006)	8.53 (0.82)	5.0	2.8	3.75
SL	3.59 (0.49)	0.99 (0.12)	0.08 (0.012)	4.26 (0.82)	3.5	5.1	3.25
JB	2.29 (0.16)	0.60 (0.06)	0.05 (0.006)	8.38 (0.95)	19.0	2.7	2.0
LB	2.87 (0.64)	0.76 (0.12)	0.05 (0.009)	6.49 (1.38)	23.5	2.5	1.0

Oxygen

Benthic respiration is the sediment oxygen demand (SOD) measured in the dark chambers (Fig. 4A). Benthic respiration rates on Day 2 ranged from –0.70 to –2.13 and –2.02 to –3.90 mmol oxygen m^{-2} h^{-1} in the control and treated chambers, respectively. While variability in benthic respiration occurred down the estuarine turbidity gradient, these results indicate consistently higher benthic respiration in the *Atrina* beds than in the adjacent bare sediments on all days (paired *t*-test $p = 0.0292$).
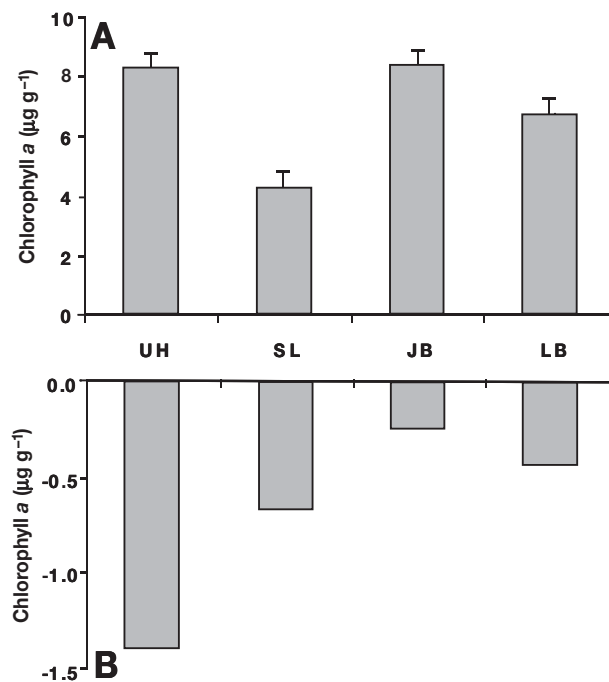

Fig. 3. (A) Average microphytobenthos biomass, as indicated by chlorophyll *a* (µg g^{-1} + SE), from all chambers at each site. (B) Net microphytobenthos biomass difference in light chambers at each site calculated as treated minus control chlorophyll *a* concentrations. Negative values indicate there was lower biomass in the treated than in the control chamber
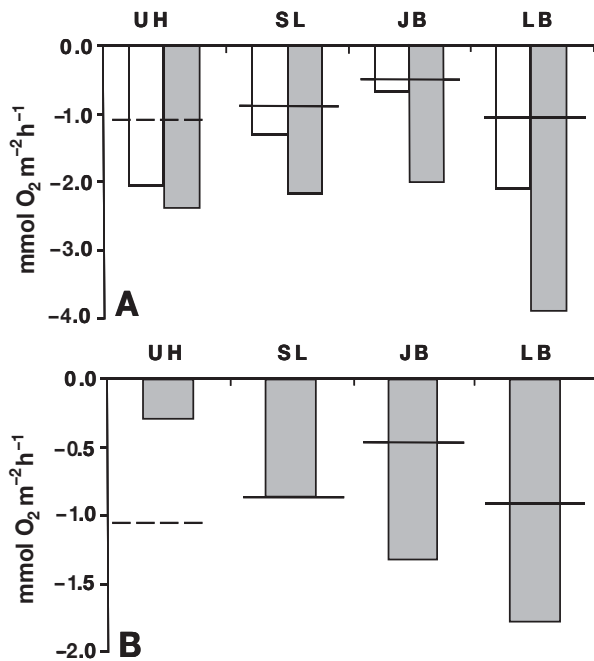
Fig. 4. *Atrina zelandica*. (A) Benthic respiration in the control (□) and treated (▨) chambers at each site, with an estimate for Site UH (———) and measured (——) areal equivalent *Atrina* respiration calculated from the *Atrina* respiration results at 4 *Atrina* m^{-2} (Table 2). (B) Net benthic respiration difference due to the presence of *Atrina*, calculated as treated minus control benthic respiration at each site. Maximum areal equivalent *Atrina* respiration is indicated as for (A). As benthic respiration is an oxygen demand, the negative results mean that there is greater benthic respiration in the treated than in the control chamber

The difference between treated and control chambers (Fig. 4B) includes direct *Atrina* respiration equivalent to benthic respiration rates of –0.54 to –1.08 mmol oxygen m^{-2} h^{-1}, calculated from the incubation results at a nominal population density of 4 m^{-2} (i.e. 1 *Atrina* per benthic chamber) (Table 2). However, while *Atrina* respiration could account for the difference at the 2 inner harbour sites (UH and SL), it could not account for all of the benthic respiration at the 2 outer harbour sites (JB and LB), suggesting that some other aspect of the *Atrina* presence may be important.

As expected, photosynthetic oxygen production occurred in the light chambers at each site and generally exceeded benthic respiration in the outer harbour sites where a higher percentage of surface irradiance reached the sediments. The difference between light and dark chamber response is assumed to be due to benthic GPP (Fig. 5A). Benthic GPP rates ranged from 1.29 to 3.35 and 0.44 to 4.17 mmol oxygen m^{-2} h^{-1} in the control and treated chambers, respectively. Overall, no consistent significant difference was observed between GPP in bare sediment and sediment with *Atrina*. However, a shift from less to more benthic

GPP in the treated than control chambers was observed down the estuarine gradient (Fig. 5B, r^2 = 0.86, p = 0.041 using ranks given in Table 6). This difference includes the direct respiration effect of *Atrina* and is consistent with greater burial of microphytobenthos within the *Atrina* beds in the inner harbour where pseudofaeces production rates are likely to be higher than in the outer harbour.

Nutrients

Benthic nutrient fluxes of DRP, TP, NH$_4$-N, NO$_3$-N, and dissolved inorganic N (DIN) (Table 7) were almost always higher in the dark than in the light chambers, and in the treated than in the control chambers at all sites. Significant differences between chambers with *Atrina* and bare chambers were found for fluxes of TP and DIN in the dark for all data (paired *t*-test p = 0.0463 and 0.0083, respectively). Significant differences were also found in the light, with DIN, NH$_4$-N and NO$_3$-N fluxes differing between chambers, with *Atrina* and bare chambers (paired *t*-test p = 0.0033, 0.0103 and 0.0414, respectively). The light–dark results are consistent with light mediation of BNF through uptake of the released nutrients by microphytobenthos at the sediment–water interface. The differences seen between the treated and control chamber results are due to the presence of the single *Atrina* in the treated chambers, and include excretion of NH$_4$-N by the *Atrina* (Table 2), as well as the effect of differences in the local infaunal abundance and microbial activity at each site.

The differences between treated and controls, seen in the DRP and TP data (Table 7), were relatively small, in the range of –1.7 to 7.5 µmol DRP m^{-2} h^{-1} and –4.6 to 7.9 µmol TP m^{-2} h^{-1}, with much of the TP difference due to the DRP component. In the light, the DRP and TP efflux from the treated chambers was consistently higher than the control for the inner 3 sites, but lower than the control at Site LB. In addition, the dark DRP and TP efflux relative to control tended to decline down-gradient for the inner 3 sites but was substantially higher at Site LB. This could not, however, be tested for statistical significance.

For DIN data (Fig. 6), the differences between treated and controls were mainly due to the NH$_4$-N component, which ranged from 5 to 81 µmol m^{-2} h^{-1} in the light (Fig. 6A), and from 22 to 146 µmol m^{-2} h^{-1} in the dark (Fig. 6B). The positive values indicate a greater efflux in the *Atrina* beds than in the adjacent bare sediments. Indications of the likely contribution from direct *Atrina* NH$_4$-N excretion were estimated from the excretion experiment results (Table 2) at a population density of 4 m^{-2}. As there was higher
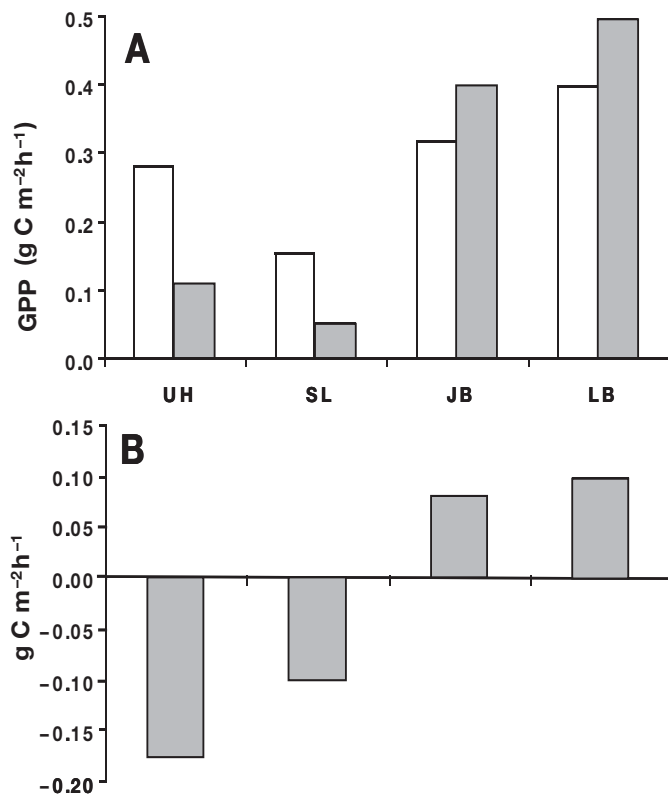
Fig. 5. (A) Benthic gross primary production (GPP) in the control (□) and treated (▨) chambers at each site. (B) Net benthic GPP difference due to the presence of 1 *Atrina*, calculated as treated minus control benthic GPP at each site. Negative values indicate greater GPP in the control chambers; positive values indicate greater GPP in the treated chambers

Table 7. *Atrina zelandica*. Excretion rates with ambient water 'A. (site)' and upper harbour water 'A. (UH)' as mean areal equivalent values at a density of 4 m^{-2}, compared with benthic nutrient fluxes (µmol m^{-2} h^{-1}) in the control (C) and treated (T), light (L) and dark (D) chamber pairs at the 4 sites along the turbidity gradient. DRP: dissolved reactive phosphorus; TP: total phosphorus; NH$_4$-N: ammoniacal nitrogen (N); NO$_3$-N: nitrate + nitrite N; DIN: dissolved inorganic N

Site	DRP		TP		NH$_4$-N		NO$_3$-N		DIN	
	C	T	C	T	C	T	C	T	C	T
UH (D)	4.3	7.4	17.8	23.3	88.4	110.2	23.1	23.1	111.6	133.3
UH (L)	2.5	7.4	16.6	22.1	20.4	69.4	6.8	32.7	27.2	102.0
SL (D)	6.5	6.5	16.1	19.4	71.4	95.7	25.7	58.6	97.1	154.3
SL (L)	1.3	6.5	19.4	21.9	12.9	94.3	10.0	31.4	22.9	125.7
A. (SL)						28.3				
A. (UH)						62.5				
JB (D)	4.9	4.2	13.3	14.7	28.0	99.4	7.8	21.7	35.7	121.1
JB (L)	2.1	6.3	14.7	22.4	28.0	40.4	4.7	10.9	32.6	51.2
A. (JB)						26.7				
A. (UH)						61.7				
LB (D)	5.4	13.1	18.4	26.1	57.8	204.1	6.8	22.1	64.6	226.2
LB (L)	6.1	4.6	19.2	14.6	37.4	42.5	6.8	17.0	44.2	59.5
A. (LB)						28.7				
A. (UH)						64.2				

turbidity at the 2 inner harbour sites (UH and SL), it is likely that *Atrina* NH$_4$-N excretion rates would be higher there than in the clearer outer harbour sites (JB and LB) (Fig. 6). However, *Atrina* NH$_4$-N excretion rates may fluctuate between these levels at Site SL with the transition from clear to turbid water on the flood and ebb tide, respectively.

Similar results were found for the nitrogen fluxes on both sampling days (although these were separated by a year) and spatial variability in the difference in fluxes generated by *Atrina* frequently appeared linked to the turbidity gradient in the harbour. ANCOVA analysis found no significant difference in the response of *Atrina*-generated benthic flux to turbidity between years (year × turbidity interaction p > 0.15 for all variables light or dark) with DIN and NH$_4$-N fluxes in the dark being predictable by turbidity (p = 0.0045 and 0.0298, respectively). There were also indications of a significant relationship with turbidity for NH$_4$-N in the light, although this was less of a gradient relationship than a difference between inner and outer estuary sites (Wilcoxon test p = 0.0558). All other relationships were non-significant (p > 0.10).

In the light (Fig. 6A), the greater efflux of NH$_4$-N at the inner than outer harbour sites may reflect the lower percentage of surface incident light reaching the sediments at those sites, and hence, less uptake by microphytobenthos. The net NH$_4$-N efflux increase attributable to the presence of *Atrina*, as estimated from the benthic chambers, is in good agreement with the likely *Atrina* NH$_4$-N excretion rates, estimated from *Atrina* excretion incubations. In the outer harbour sites, the NH$_4$-N efflux, estimated from the benthic chambers, was smaller than the likely *Atrina* NH$_4$-N excretion rates, indicating a large sediment nitrogen demand, probably from the microphytobenthos in the higher light environment (e.g. Sundbäck et al. 2004).

In the dark (Fig. 6B), benthic chamber results showed a smaller net efflux of NH$_4$-N than the likely *Atrina* NH$_4$-N excretion rates at the inner harbour sites, but a much greater net efflux than the likely *Atrina* NH$_4$-N excretion rates at the outer harbour sites. A similar pattern was observed in the preliminary experimental results in 2001 (Fig. 6B). While the reduction in microphytobenthos nutrient uptake in the dark would account for the outer harbour results, the inner harbour results may indicate some changes in biogeochemical processes within the sediments (e.g. Anderson et al. 2003).
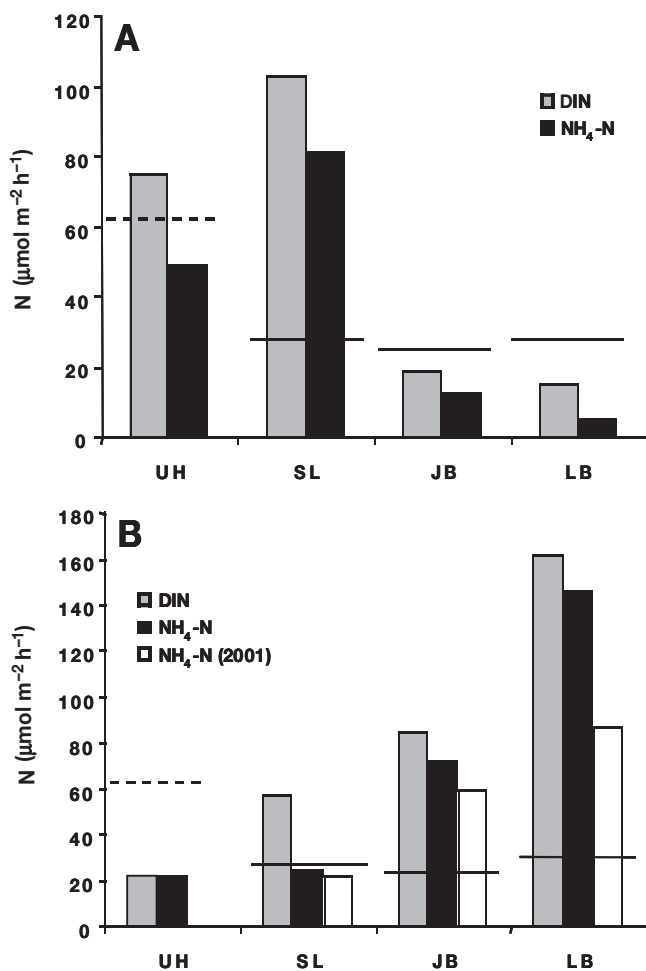
Fig. 6. Net effect of the presence of *Atrina zelandica* on the dissolved inorganic nitrogen (DIN) and ammoniacal nitrogen (NH₄-N) effluxes (A) in the light, and (B) in the dark chambers at each site. Dark NH₄-N effluxes measured in 2001 show a similar pattern to the 2002 results. Differences calculated as treated minus control efflux rates at each site. Likely equivalent areal *Atrina* NH₄-N excretion rates estimated for Site UH (----) and as a measure for the other 3 sites (——), calculated from the excretion incubation results (Table 2) for a density of 4 *Atrina* m⁻²

The presence of a NO_3-N efflux in the chambers indicates that some of the NH_4-N released from the sediments was being nitrified. This also implies that denitrification rates were less than nitrification rates. The differences, relative to controls, seen in the NO_3-N data (Fig. 7) show a consistent pattern of greater nitrification in the treated than control chambers, except at Site UH in the dark, where the nitrification rates were the same.

Whereas the NO_3-N component is about 10 to 25% of the DIN efflux, an estimate of the absolute DIN efflux cannot be made as we made no measurement of denitrification rates. The apparent decrease in NO_3-N

component down the estuarine gradient cannot be interpreted as reduced nitrification rates as it could also indicate a faster denitrification rate and, thus, less of the nitrified NH_4-N would remain in the water column as free NO_3-N. However, a consequence of faster denitrification rates would be an overall reduction in the total nitrogen in the sediments down the estuarine gradient and this is seen in the % N data (Tables 4 & 6).

DISCUSSION

The results from this study indicate that there are potentially large differences between the BNF from beds of the pinnid bivalve *Atrina zelandica* and the adjacent bare sediments, as well as differences along the turbidity gradient in Mahurangi Harbour. Our results indicate a step-wise change in the effects of suspended solids concentrations between the 2 inner and 2 outer harbour sites rather than a continuous gradient downstream. What are the likely causes of these differences and what is the effect of the presence of *Atrina* beds on the nutrient supply to this harbour?

Nutrient supply to Mahurangi Harbour is from land, via stream inflows and surface runoff, the coastal water outside the harbour, via tidal exchange, and mineralisation of accumulated sediment and suspended solids within the harbour as BNF. Indications of nutrient supply from land drainage and BNF versus tidal exchange can be seen in the water column nutrient data (Table 1), which show a decline in NH_4-N and TP from the inner to outer harbour. The implication being that tidal exchange from the coastal waters in summer is nutrient-deficient as seen elsewhere around the New Zealand coast (e.g. Gibbs & Vant 1997, Zeldis 2004). The BNF and land drainage origin of the water-column nutrients is also implied by the chlorophyll *a* concentrations, which increased by about 1 mg m⁻³ in the light bottles over the 5 h incubation at the 3 inner harbour sites, and substantially less at the harbour entrance (Table 1).

The release of nutrients from the sediments, following mineralisation, occurs throughout the harbour, and the observed nutrient concentration differences between sites may be a function of differential dilution of BNF as the water becomes deeper towards the harbour entrance. Sequestering by microphytobenthos may also have a spatial effect as has been seen in estuaries and fjords elsewhere (e.g. Sundbäck et al. 2004), although there was little spatial difference in microphytobenthos species composition or biomass, which averaged ca. 6.8 µg chlorophyll *a* g⁻¹ across the 4 sites. This is equivalent to ca. 85 mg chlorophyll *a* m⁻² and is comparable with the average benthic biomass of 97.5 mg chlorophyll *a* m⁻² in summer for the sediments
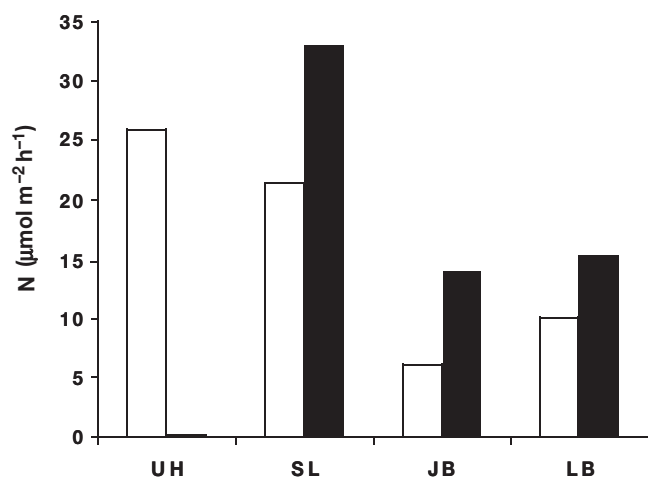
Fig. 7. Net effect of the presence of *Atrina zelandica* on the nitrate + nitrite nitrogen (NO_3-N) efflux in the light (□) and dark (■) chambers at each site

of nearby Manukau Harbour (Cahoon & Safi 2002), but is at the higher end of the range (11 to 102 mg chlorophyll *a* m^{-2}) reported in Gullmar Fjord, Sweden (Sundbäck et al. 2004).

While our *in situ* benthic chamber experiments examined the differences between bare sediment and sediment with *Atrina*, it is obvious that *Atrina*, which are suspension feeders, have a direct influence on water-column nutrient dynamics independent of sediment nutrient release. The laboratory respiration and excretion incubations demonstrated that, while the respiration of an individual *Atrina*, at 0.5 to 1.0 mg oxygen h^{-1} in summer, was only slightly affected by changes in suspended solids concentrations, their NH_4-N excretion rates increased dramatically from about 0.1 to about 0.22 mg h^{-1} when exposed to the highly turbid inner harbour water, possibly associated with higher pseudofaeces production. This response to changes in suspended solids concentrations implies that *Atrina* can react quickly to changing environmental conditions.

A response to increased turbidity was also apparent in the benthic chamber results when looking at the net effect of the presence of *Atrina* (Fig. 6). At the more turbid inner harbour sites, the net NH_4-N increase in the light chambers was comparable with *Atrina* excretion rates in turbid water, as measured in the laboratory incubations using similar water. This indicates that the apparent BNF increase at these sites was probably entirely attributable to *Atrina* excretion during the day. However, at the less turbid outer harbour sites, the net NH_4-N increase in the light chambers was less than half the *Atrina* excretion rates measured in the laboratory incubations with similar water. This indicates that the sediments in the outer harbour are likely to be a

sink for nutrient nitrogen from the water column in daylight, implying either enhanced uptake by microphytobenthos or microbial activity (e.g. denitrification) within the sediments.

Resolution of this issue is suggested from the dark chamber results (Fig. 6B). In contrast to the large net NH_4-N increase in the light chambers at the turbid inner harbour sites, in the dark, the net NH_4-N increase was substantially less than the *Atrina* excretion rates measured in the laboratory incubations. As *Atrina* excretion rates are unlikely to be affected by a change in light, the reduced NH_4-N efflux in the dark at these sites implies an increase in nitrification and denitrification. Evidence of enhanced nitrification in the *Atrina* beds, especially at the inner harbour sites, can be seen in the net NO_3-N efflux results (Fig. 7). Whereas the presence of NO_3-N is a function of the balance between nitrification and denitrification, the absence of NO_3-N in the benthic environment may indicate that denitrification rates exceed nitrification, rather than a lack of nitrification. Consequently, the loss of NO_3-N at Site UH in the dark most likely indicates an increase in denitrification rate.

In the dark at the outer harbour sites, the increase in net NH_4-N efflux relative to the light chamber results (Fig. 6) is consistent with there being little or no microphytobenthos nutrient uptake in the dark. This seems contrary to the recent findings of Anderson et al. (2003), who suggest that dark uptake by microphytobenthos is likely to be an important sink for mineralised N. Our results do not deny this possibility but imply that the true N mineralisation rate in Mahurangi Harbour sediments is much higher than the dark uptake rate, and the NH_4-N efflux observed is a net excess. Our net NH_4-N and NO_3-N efflux results are comparable with the efflux rates measured in light and dark at the shallower depths in Gullmar Fjord in spring but are higher than those measured in late summer (Sundbäck et al. 2004).

As the dark net NH_4-N efflux (treated minus control chamber results) at the outer harbour sites is substantially greater than the *Atrina* excretion rates, it is likely that most of the increase is due to differences in the sediment caused by the presence of the *Atrina*. The similar pattern of net NH_4-N efflux in the dark, down the turbidity gradient, measured the previous summer indicates that this spatial difference is unlikely to be a transient feature.

Our results demonstrate that BNF are greater from *Atrina* beds than bare sediments in the clearer outer harbour waters at night. The marked difference between light and dark results, however, implies that nutrients released from organic decomposition and mineralisation within the sediments are being microbially (nitrification–denitrification) and biologically

(microphytobenthos uptake in the light and dark) sequestered before reaching the overlying water column.

The results for the more turbid inner harbour sites are less obvious, although the high net NH_4-N efflux in the light was attributable to *Atrina* excretion. Differences between light and dark may be associated with the higher rates of biodeposit (pseudofaeces) production by *Atrina* in turbid water (Ellis et al. 2002). The flow-on effect of higher biodeposit production is the potential to bury the microphytobenthos and reduce bioturbation. Previous studies in Mahurangi Harbour (Cummings et al. 1998, 2001, Ellis et al. 2000, Norkko et al. 2001, Hewitt et al. 2002) have demonstrated the effect of *Atrina* beds on increasing diversity, and changing community composition and functioning of the macrofauna (both as in- and epifauna). While the epibenthos affects the water column above the sediments, burrowing macrobenthos and infauna can impact on the nutrient dynamics within the sediments (Quijón et al. 1996, Gilbert et al. 1998, Newell et al. 2002). Some of these effects may be responsible for the spatial differences down the turbidity gradient seen in several of the other parameters measured.

Evidence of this can be seen in the GPP results (Fig. 5A), where GPP is lower in the *Atrina* beds than adjacent bare sediment at the inner harbour sites. This is consistent with burial by enhanced pseudofaeces production. As *Atrina* respiration rates measured in the laboratory incubations are equivalent to an areal sediment respiration rate of about –0.12 g C m^{-2} d^{-1}, most of the negative GPP at the inner harbour sites can be accounted for by *Atrina* respiration (Fig. 5B). This is consistent with the net NH_4-N efflux being accounted for by *Atrina* excretion. Burial by pseudofaeces would account for the small decrease in estimated microphytobenthos biomass in the *Atrina* beds relative to the adjacent bare sediments at these sites. In contrast, at the outer harbour sites, positive net GPP[2] rates indicate a substantial increase in microphytobenthos biomass in the *Atrina* beds relative to adjacent bare sediments. However, this is not consistent with the net microphytobenthos biomass estimates, which indicate a slight biomass decrease in the *Atrina* beds relative to adjacent bare sediments at these sites. Consequently, as there was no apparent difference in the species composition of microphytobenthos, the additional GPP is likely to reflect the production due to photosynthesis by epibenthos within the *Atrina* beds.

While epibenthos may photosynthesise, they are unlikely to alter the nutrient efflux leaving the sediments because they may not be in contact with those sediments. However, they may uptake those nutrients from the water column within the benthic chamber. This means that the degree of GPP increase in the *Atrina* bed relative to adjacent bare sediment may reflect the confinement of nutrients within the benthic chambers, nutrients which might otherwise have dispersed into the overlying water. Our data show the likely epibenthos GPP to be 0.15 to 0.2 g C m^{-2} d^{-1} for an uptake of about 0.5 mmol N m^{-2} d^{-1} giving a C:N ratio in the order of 21 to 28.5. As C:N ratios for attached macroalgae are in the order of 20, this uptake is consistent with epibenthos growth, which could account for the additional nutrient loss in the light chambers.

There was 35% less organic matter in the outer than inner harbour sediments and a similar reduction in C and N content (Table 6). This suggests either less sedimentation or greater removal by microbial activity in the outer harbour sediments. Stable isotopic composition of the sediments suggest substantial ^{13}C enrichment in the outer harbour sediments relative to the inner harbour (Table 5), which indicates greater or faster microbial processing. The apparent reduction in organics content may, thus, be attributable to microbial activity. The enhanced nutrient release within the *Atrina* beds at the outer harbour sites would also be consistent with higher bioturbation and infaunal abundance.

While it is not possible to produce a full nutrient budget for Mahurangi Harbour from the data available, we can produce an estimate of the potential effect of the

Table 8. Simple nutrient budget used to estimate the relative importance of *Atrina zelandica* beds to the water column nutrient supply for primary production. Efflux values are net, and include the effects of coupled nitrification–denitrification and uptake by benthic microphytes. Sediment areas are estimated from Hewitt et al. (2002)

		Sediment area (km^2)	
		Turbid zone	Clear zone
Bare sediment		14	4
Atrina beds		2	5
Net DIN efflux (kg N)			
Bare sediment	(day[a])	70	30
	(night[a])	200	30
Atrina beds	(day[a])	230	280
	(night[a])	195	585
Net nutrient supply to Mahurangi Harbour			
		Mass (kg N d^{-1})	% Total
River inflow (est.)		3.5	0.2
Bare sediment		330	20.3
Atrina beds		1290	79.5
Total		1623.5	
[a]day:night ratio = 0.6:0.4			

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[2]Note that the net GPP rates at the outer harbour sites include the *Atrina* respiration equivalent of –0.12 g C m^{-2} d^{-1}

Atrina beds on the nutrient supply (Table 8) and, thus, the relative importance of *Atrina* to the nutrient supply for primary production within the harbour. If we assume an *Atrina* density of 20 m^{-2} for about 7 km^2 of outer harbour, based on the spatial distribution and abundance map of Hewitt et al. (2002), and a direct proportional increase in the light and dark BNF rates from 4 *Atrina* m^{-2} (Table 7), and a summer river inflow of about 3.5 kg DIN d^{-1} (R. Wilcock pers. comm.), we estimate that *Atrina* beds contribute up to 80% of the daily DIN supply to the harbour (Table 8). A similar calculation without *Atrina* (using bare sediment BNF rates) suggests an estimated 75% reduction in the summer DIN supply.

We recognise that these calculations (Table 8) have potentially large error terms, and they are not intended to be used as a nutrient budget. However, they demonstrate that the *Atrina* beds in Mahurangi Harbour potentially play an important role in the primary production that supports the aquaculture of Pacific oysters in this harbour. Without the *Atrina* beds, primary production would most likely decrease dramatically. As such changes to potential primary production would adversely affect the aquaculture industry in Mahurangi Harbour, the present decline of the *Atrina* beds due to increasing turbidity from catchment development is of major concern.

CONCLUSIONS

The presence of *Atrina* beds has an effect on the BNF in Mahurangi Harbour that varies along a turbidity gradient. In the highly turbid inner harbour, *Atrina* enhance sedimentation through their biodeposits. These biodeposits have the potential to smother microphytobenthos, thus reducing uptake and enhancing pelagic nutrient concentrations from *Atrina* excretion during the day. However, at night, the biodeposits potentially enhance nutrient loss through enhanced denitrification. With the decline in *Atrina* populations in the inner harbour, daytime nutrient nitrogen supplies are likely to decrease markedly but may increase slightly at night.

In the outer harbour, the presence of *Atrina* beds produces a small overall increase in the nutrient nitrogen supply during the day, but a substantial increase in BNF at night. In contrast with the inner harbour sites, where the nutrient increase is directly from the *Atrina* excretion, nutrient increases are a function of microbial activity in the sediments associated with enhanced bioturbation in the outer harbour. With *Atrina* beds, there is a marked increase (almost double) in BNF from the beds at night relative to adjacent bare sediments and, consequently, highest nutrient availability is likely to occur early in the morning before sunrise. Without *Atrina*

beds, the present strong diurnal cycle of nutrient supply would weaken and overall primary production in the outer harbour would most likely reduce substantially.

In terms of nutrient supply in Mahurangi Harbour in summer, we estimate that *Atrina* beds potentially account for up to 80% of the nutrients available for primary production, and without them, the daily nutrient availability could decrease by as much as 75%.

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