

Benthic–pelagic coupling and suspension-feeding bivalves: Linking site-specific sediment flux and biodeposition to benthic community structure

Abstract—Suspension-feeding bivalves play an important role in coastal ecosystems by affecting near-bed hydrodynamics and, subsequently, rates of biodeposition. We designed a high-resolution field study to investigate rates of sedimentation and biodeposition around individuals within beds of the large pinnid bivalve, *Atrina zelandica*, and to link these rates with sediment biogeochemical characteristics and macrofaunal community structure. The study was conducted at three sites arrayed along a gradient of increasing suspended seston concentration, enabling us to assess changes in the strength of the *Atrina*–macrofauna interaction with background sedimentation. Sedimentation rates and inputs of organic carbon and nitrogen were higher close to individual *Atrina* (≤ 10 cm) compared to further away (> 30 cm). Seafloor sediments nearer *Atrina* were enriched in carbon and nitrogen and had more diverse and abundant macrofaunal assemblages. The strength of this interaction decreased with increasing background sedimentation. Although other mechanisms, both biotic and abiotic, may explain some of these patterns, we have identified variations in macrofaunal community structure that at least partly can be linked to site-specific sedimentation, at the small scale of single *Atrina*, nested within the larger landscape scale of *Atrina* beds, emphasizing *Atrina*'s role in habitat modification, both structurally and functionally.

Suspension-feeding bivalves play a pivotal role in coastal soft sediment systems through their influence on benthic–pelagic coupling and nutrient cycling (Dame 1993; Wildish and Kristmanson 1997). By altering their physical habitat, bed roughness, and water flow over the seabed (Frechette et al. 1989; Green et al. 1998), the bivalves modify the depositional (e.g., biodeposition) and erosional (e.g., bioresuspension) processes occurring at the seafloor (Graf and Rosenberg 1997). Biodeposition in beds of suspension-feeding bivalves results from the active filter feeding by the bivalve, which leads to nondigested material being excreted to the sediment surface as feces and pseudofeces. These processes can result in local deposition rates that exceed that of passive physical sedimentation (Verwey 1952; Dame 1993). Biodeposits can be rich in carbon and nitrogen (Kautsky and Evans 1987), both of which enrich sediments and stimulate microbial growth (Grenz et al. 1990; Stoeck and Albers 2000), and may thus provide an important resource for surrounding benthos (Marsh and Tenore 1990). Experimental manipulations of suspension feeders have demonstrated variable effects on associated infauna (Olafsson et al. 1994). Given their potential role in elevating benthic fluxes to the seafloor, we would expect clearer effects of suspension feeders on benthic communities. Earlier density manipulation experiments and surveys with the large suspension-feeding bivalve, *Atrina zelandica* (Gray), have demonstrated significant effects on surrounding macrobenthic communities, although the strength and direction of these effects var-

ied in space and time (Cummings et al. 1998, 2001; Thrusch et al. in press). Nevertheless, local hydrodynamic conditions and the spatial arrangement of individuals within beds of these suspension feeders were found to be important variables explaining site differences. Although not measured, local variations in fluxes of sediments and biodeposits to the seafloor were proposed as important variables affecting macrobenthic community composition. Biodeposits have also been implied as being important in interactions between suspension feeders and surrounding macrofauna in several other studies (e.g., Commito and Boncavage 1989; Dittmann 1990; Ragnarsson and Raffaelli 1999). However, no previous studies have measured or demonstrated a link between the site-specific sediment fluxes around individuals within patches of suspension-feeding bivalves and the structure of macrobenthic communities.

Apart from the local effects in the vicinity of individuals or patches due to interactions between suspension feeders and local hydrodynamic conditions, broader scale changes may also modify the role of suspension feeders. Gradients in suspended sediment flux and sediment grain size and organic content are common in coastal environments. For example, increased concentrations of sediments in the seston can significantly change the quantity and quality of biodeposits by increasing pseudofeces production (Dame 1993; Iglesias et al. 1996); hence, such broad-scale gradients are predicted to affect the strength of the suspension feeder–macrofauna interaction.

In this paper, we tested predictions about site-specific links between sediment flux and macrobenthic communities around individuals within patches of the large suspension-feeding bivalve *A. zelandica*. We designed a high-resolution field study to test the following predictions: (1) increased fluxes of sediments and biodeposits occur around individual suspension feeders, (2) increased biodeposition alters sediment biogeochemical characteristics and elevates carbon and nitrogen levels, (3) macrobenthic communities near individual suspension feeders are distinctly different from those in bare patches, and (4) effects are site-specific due to local variations in seston concentration. To address the latter, we chose our sites to encompass a range of environmental conditions along a gradient of increasing suspended sediment concentration.

Test species and study sites—*A. zelandica* (Gray) is a large (up to 30 cm long) suspension-feeding pinnid bivalve common in the subtidal soft sediments of north-eastern New Zealand. These large bivalves live partially buried in the substrate with their anterior portion protruding above the sediment surface and often form extensive biogenic reefs (e.g., 100–1,000 m²) on the seafloor. They live in a wide variety of coastal and estuarine habitats, which encompass

sandy to muddy substrates and wave- to tidally dominated flows. The study was conducted in beds of *Atrina* at three sites (4–7-m depth) on the East Coast of the North Island, New Zealand. Two sites, Te Kapa and Jamieson Bay, were situated within Mahurangi Harbor, and one site was on the adjacent coast in Martins Bay. The sites were positioned along a gradient of increasing suspended sediment load, from an average total particulate matter (TPM) content of 38 mg L⁻¹ at Martins Bay, to 44 at Te Kapa and 49 at Jamieson Bay (measured over one tidal cycle 10 cm above the bed). Extensive beds of *Atrina* were dominant features at all sites, with mean densities ranging from four to eight individuals per square meter. Martins Bay is the most exposed site physically, characterized by fine and medium sands and comparatively high macrofaunal diversity. Tidal flows at this site are weak (max = 0.05 m s⁻¹), and water movement is dominated by waves. Inside the harbor, at Te Kapa and Jamieson Bay, sediments are comprised of silt and fine sand; these sites have lower numbers of taxa but higher numbers of individuals than Martins Bay. Circulation within the harbor is dominated by semidiurnal tides, and the water column is typically well mixed. Tidal flows at the sites attain maximum speeds of 0.20 m s⁻¹ during spring tides and around 0.10 m s⁻¹ during neap tides. Deposit feeders dominate the benthic community, with their relative proportion increasing with suspended sediment load.

Study design and sampling—At each site, divers established a 20-m transect through an *Atrina* bed, oriented parallel to the dominant tidal flow. This scale of sampling encompassed the small-scale patchiness at each site, enabling us to locate samples near individual *Atrina* and in adjacent bare patches. Along the 20-m transect, 10 locations were chosen within 10 cm of an individual *Atrina*, and 10 locations were chosen in a bare sediment area at least 30 cm away from any *Atrina*. At each location, two sediment traps, filled with clean seawater and capped, were carefully inserted into the sediment: one positioned so that its opening was 12 cm above the bed, i.e., 3–4 cm above *Atrina* (hereafter “high trap”), and the other, so that its opening was 1 cm above the bottom (hereafter “low trap”). Thus a total of 40 sediment traps were deployed at each site. The traps were 20 cm in length and 2.8 cm in diameter (7:1 aspect ratio). The caps were carefully removed, and the traps were left for 48 h during a mean tide. They were then recapped and retrieved, with care taken to prevent incursion of sediments disturbed by the divers. Surficial sediment samples were collected adjacent to each low trap at each location for the analysis of organic content, particulate organic carbon (POC), and particulate organic nitrogen (PON). Surficial sediment was collected by scraping off the top 0.5 cm of sediment from a 10-cm² area. To assess the benthic community at each location, core samples (3.4 cm in diameter; 5 cm deep) were collected near each low trap. This sampling strategy enabled us to link site-specific sediment flux (as measured over the 48-h period at mean tide), biogeochemical conditions in the sediment, and macrobenthic community structure at each location (i.e., 10 *Atrina* and 10 bare locations) within each site.

Analysis of benthic macrofauna, biodeposits, and sediments—Macrofaunal cores were sieved (250- μ m mesh), preserved in 70% isopropyl alcohol, and stained with 0.1% rose bengal. Macrofauna in each core were identified to the lowest taxonomic level practical and counted. Four macrofaunal aggregate groups (number of taxa, number of individuals, number of deposit feeders, and number of scavengers and grazers) were compiled for each core. Common taxa (i.e., mean abundance = two or more individuals per core at least at one site) and total number of rare taxa (i.e., mean abundance = less than one individual per core at all sites) were also calculated. The material collected in each sediment trap was dried at 60°C for 48 h and weighed. The sediment trap material was further analyzed for POC and PON. The surficial sediment samples were analyzed for organic matter, POC, and PON. POC and PON of sediments and biodeposits were determined on dried samples that had been finely powdered and homogenized. A subsample was combusted using a Perkins-Elmer CHN Elemental Analyzer after removal of carbonates by acidification with 25% HCl.

Statistical analysis—Sediment deposition, total amount of POC, and total amount of PON of the sediment collected in the traps were analyzed using three-way analysis of variance. Height of the trap above the bed (height), location of the trap either next to an *Atrina* or in a bare area of sediment (location), and site were all fixed factors. Site was included as a fixed rather than a random factor, as the sites had been deliberately chosen to represent a range of environmental conditions, which we expected to affect our results. To meet the assumptions of normality and homogeneity of variance (Shapiro-Wilk and *F*-max tests, respectively), data were ln-transformed. The three-way analyses of variance for all variables demonstrated significant interactions with trap height ($P < 0.05$; see Web Appendix 1 at http://www.aslo.org/lo/toc/vol46/issue_8/2067a1.pdf). Thus, two-way analyses of variance were carried out for the two heights separately. Where significant location–site interactions were found, sites were analyzed separately, and differences in means were tested for with contrast statements (SAS/Insight 1993). Otherwise, a significant result ($P < 0.05$) was followed by a Ryan-Einot-Gabriel-Welsch multiple range test for differences in main effects. Surface sediment POC and PON concentrations were analyzed by two-way analysis of variance, with site and location as fixed factors. Data were ln-transformed to meet assumptions of normality and homogeneity of variance. Macrofaunal abundance data were analyzed using generalized linear models (McCullagh and Nelder 1989) to account for different error structures. Three of the four macrofaunal aggregate groups did not require transformation or a non-normal error structure. Numbers of scavengers and grazers and the few common taxa—exogonid and polydroid polychaetes, phoxocephalid amphipods, and the cumacean *Hemileucon* sp.—were all analyzed using a Poisson error structure and a log-link function (SAS/Insight 1993). As the polydroids and exogonids were overdispersed, a quasi-likelihood function was used in their analysis. Macrofaunal community structure was assessed using the statistical package PRIMER (e.g., Clarke 1993). Differences in assemblages found near *Atrina* and in bare sediment at each site were

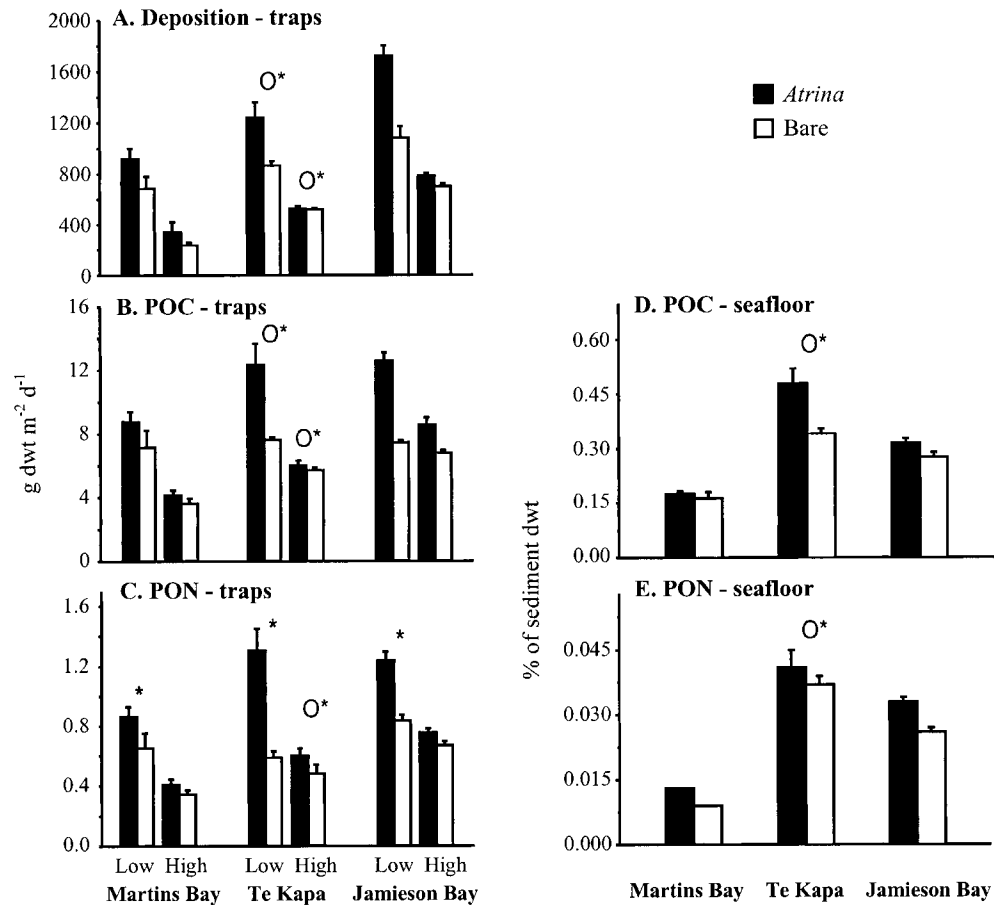


Fig. 1. Material collected in the low and high sediment traps over 48 h at each site and sediment characteristics of the surrounding sediment close to *Atrina* and in bare areas (i.e., location). (A) Total amount of deposited material. (B) Total influx of organic carbon. (C) Total influx of organic nitrogen. (D) Percentage organic carbon at the seafloor. (E) Percentage organic nitrogen at the seafloor. Values given are mean \pm standard error. O* = significant differences between locations over all sites; * = significant difference between location at a specific site. Significance levels for A, B, and C come from a two-way analysis of variance carried out for each trap height separately (see Web Appendix 1 at http://www.aslo.org/lo/toc/volLxx/issue_x/xxxxxa1.pdf for full details on statistics).

investigated using Bray–Curtis similarities calculated on the raw data and nonmetric multidimensional scaling. The statistical significance of these differences was analyzed using the ANOSIM routine within PRIMER.

Sediment fluxes and biodeposition—High local rates of sedimentation occurred near *Atrina*. The mass of sediment material collected in the low traps was always significantly higher ($P = 0.0001$; Web Appendix 1) near *Atrina* than in the bare areas (Fig. 1A). Also, the amount of sediment collected in the high traps differed with trap location at all sites ($P = 0.0292$; Fig. 1A). Overall differences were observed in the amount of sediment collected at each site, with the most collected at Jamieson Bay and the least collected at Martins Bay. This difference was observed at both trap heights, reflecting the differences in sediment loading (TPM) between sites. All the material collected in the traps was fine grained, with the low traps close to *Atrina* containing mostly

mucous-like material resembling that observed as being biodeposits.

Biogeochemical characteristics of the trap material and seafloor sediments—The total organic carbon and nitrogen influx was significantly higher ($P < 0.05$) near *Atrina* than in bare areas in both the low and high traps (Fig. 1B,C; Web Appendix 1). Total amounts of organic carbon and nitrogen deposited were highest at Jamieson Bay and lowest at Martins Bay. Although the analysis of variance detected a site–location interaction for the total amount of organic nitrogen in the low traps ($P = 0.0384$), this was not a change in direction merely in strength, with most organic nitrogen found near *Atrina* at each site (Fig. 1B,C). Similarly, seafloor sediments near *Atrina* had a higher percentage organic carbon and nitrogen than those in the bare areas ($P = 0.0005$ and 0.0001 , respectively; Fig. 1D,E).

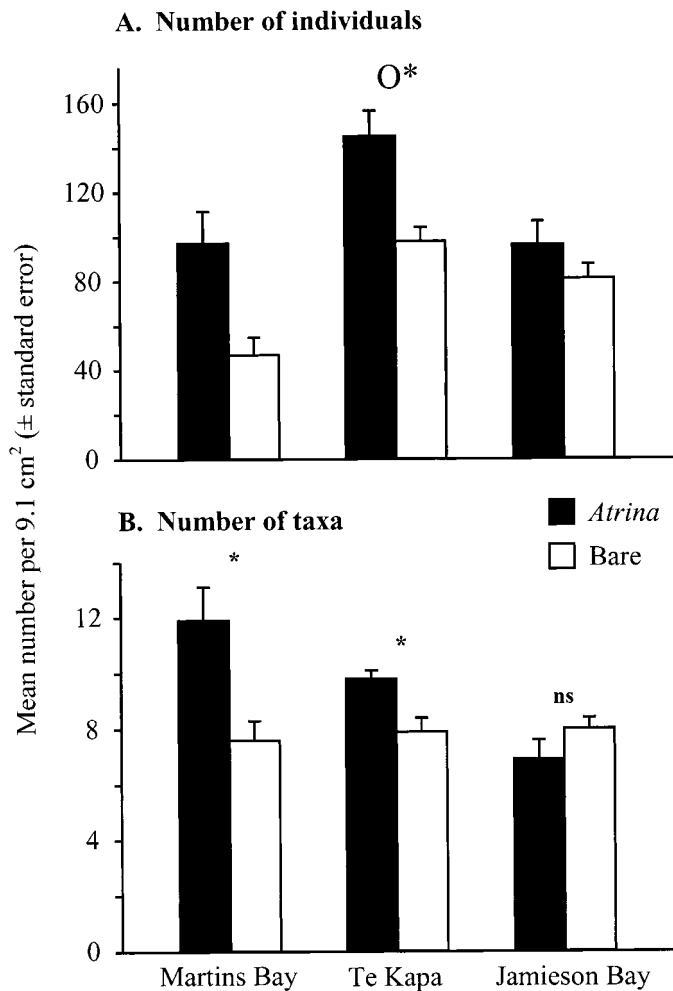


Fig. 2. Mean number of individuals (A) and number of taxa (B) at each site close to *Atrina* and in bare areas (i.e., location). O* = significant differences between locations over all sites; * = significant difference between location at a specific site; ns = not significant (see Web Appendix 1 at http://www.aslo.org/lo/toc/vol_xx/issue_x/xxxxx1.pdf for full details on statistics).

Patterns in benthic macrofauna distribution—Significantly higher numbers of individuals were found near *Atrina* than in bare areas at all sites ($P = 0.0001$; Fig. 2A; Web Appendix 1). This difference was especially strong at Martins Bay (52% more individuals were found near *Atrina*; Fig. 2A), whereas differences were less pronounced at Jamieson Bay (i.e., 16%; Fig. 2A). The average number of taxa was also significantly higher near *Atrina* at Martins Bay and Te Kapa ($P = 0.0057$ and 0.0094 , respectively); however, an opposite, but nonsignificant ($P = 0.2116$), pattern was observed at Jamieson Bay (Fig. 2B). In terms of total numbers of taxa and rare taxa, more were recorded near *Atrina* at all sites (Table 1). Deposit feeders dominated the macrofaunal communities at each site and were consistently found in higher numbers close to *Atrina* compared to the bare areas ($P = 0.0002$; Table 1). The deposit feeders consisted mainly of a suite of surface-dwelling ostracod species. Scavengers and grazers were significantly more abundant close to *Atrina* than in bare areas at Martins Bay and Te Kapa but not at Jamieson Bay ($P = 0.0047$, 0.0109 , and 0.2175 , respectively; Table 1). For the four common taxa, all of the significant differences detected involved higher abundances near *Atrina* than in bare areas (Table 1). *Hemileucon* sp. was found only at Te Kapa, with no significant differences in abundance found between *Atrina* and bare areas ($P = 0.8925$). Only polydorid polychaetes were found in higher abundances in bare areas away from *Atrina*, but these differences were not significant ($P = 0.9293$; Table 1). The multivariate analysis showed distinct differences in macrobenthic community composition between sites. Within each site, the strength of difference in assemblage composition near and away from *Atrina* decreased moving up the sedimentation gradient from Martins Bay to Jamieson Bay. In Martins Bay, the assemblages found near *Atrina* were distinctly different from those in bare sediment (Fig. 3; ANOSIM, $P < 0.001$). While similar, significant differences were also found at Te Kapa ($P < 0.001$); however, these differences were less pronounced (Fig. 3). At Jamieson Bay, no significant difference was detected ($P = 0.420$).

Discussion—Our results suggest apparent and consistent effects of *Atrina* on benthic macrofaunal assemblages. Their

Table 1. The total numbers of taxa, rare taxa, and patterns of abundance for aggregate macrofaunal groups and common taxa around *Atrina* and in bare areas. Values given are mean number per 9.1 cm² core (\pm SE). O* = significant differences between locations over all sites; ss = significant difference between location at a specific site (difference indicated by *); s = taxa occurred at one site only. See Web Appendix 1 at http://www.aslo.org/lo/toc/vol_46/issue_8/2067al.pdf for full details on statistics. Rare taxa = taxa with mean abundances of less than one individual per core at all sites.

	Martins Bay		Te Kapa		Jamieson Bay	
	<i>Atrina</i>	Bare	<i>Atrina</i>	Bare	<i>Atrina</i>	Bare
Total taxa	45	24	19	15	23	18
Total rare taxa	36	11	14	7	14	11
Deposit feeders	O* 65.6 (6.5)	41.9 (7.5)	127.0 (10.0)	87.6 (6.5)	90.6 (9.5)	76.3 (6.5)
Scavengers and grazers	ss 30.3 (11.6)*	4.6 (1.4)	15.8 (2.3)*	9.4 (1.3)	3.8 (1.0)	2.6 (0.2)
Ostracods	O* 52.6 (6.1)	28.4 (5.7)	121.0 (9.8)	78.7 (4.9)	89.1 (9.1)	74.8 (4.9)
Exogonids	ss 24.2 (10.3)*	2.5 (1.0)	0.6 (0.3)	0.5 (0.1)	2.1 (1.1)	1.9 (0.3)
Polydorids	2.0 (0.6)	7.7 (3.4)	5.4 (1.1)	8.1 (3.6)	0.4 (0.2)	0.2 (0.1)
<i>Hemileucon</i> sp.	s 0	0	11.2 (2.3)	7.9 (1.5)	0	0
Phoxocephalids	O* 0.5 (0.3)	0.5 (0.2)	2.8 (0.4)	0.8 (0.3)	0	0

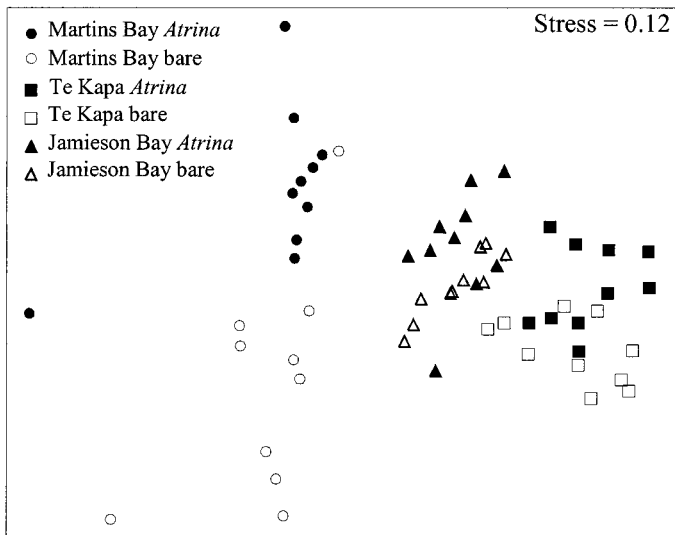


Fig. 3. Ordination plot of untransformed community data (i.e., relative species abundance) for each location (*Atrina* and bare) and site produced by nonmetric multidimensional scaling. The axes have no labels, as they have no meaning in absolute terms.

effects were associated with modification of the local habitat due to biologically mediated sedimentation around individual bivalves. We found higher sedimentation rates and inputs of organic carbon and nitrogen close to individual *Atrina* (≤ 10 cm) compared to further away (>30 cm) in bare areas. Further, seafloor sediments close to *Atrina* were enriched in carbon and nitrogen and had greater faunal abundance and diversity compared to those in bare areas away from *Atrina*. Deposition of sediment and biodeposits varied across sites in response to increasing background TPM in the seston, decreasing the interaction strength between *Atrina* and the surrounding macrofauna. Thus, although no direct causal relationship can be proved, all of our initial predictions were supported. Carbon- and nitrogen-rich deposits provide a valuable food source for benthic deposit feeders, which often rely on sedimentation material for their diets (Lopez and Levinton 1987). Deposit feeders can exhibit quick responses to inputs of organic matter (Whitlatch 1980), and their abundances are generally highly correlated with the organic content of the sediment (Pearson and Rosenberg 1978). Deposit feeders were the numerically dominant group at all sites in our study.

The scale of patchiness in food resources around individual *Atrina* will be influenced by hydrodynamic conditions. Patches of organic matter resulting from passive accumulation in relation to surface roughness of the sediments have been demonstrated in both shallow coastal waters (Eckman 1979; Van Blaricom 1982) and the deep sea (Snelgrove et al. 1992; Grassle and Grassle 1994). Laboratory and field studies have shown that boundary flow conditions and depositional and erosional processes are modified around individual structures (e.g., tubes [Eckman 1985]; bivalves [Ertman and Jumars 1988]; and feeding pits [Yager et al. 1993]) and over patches of structures (e.g., bivalve beds [Frechette et al. 1989; Green et al. 1998]). However, no studies have explicitly investigated deposition processes around individuals within larger patches in field conditions. Finding vari-

ations in fluxes of sediments and biodeposits associated with *Atrina* individuals points to spatial variation in resources occurring within *Atrina* beds. These small-scale variations in the resource distribution may explain some of the variable results, and lack of effects, found in suspension feeder manipulation studies (Olafsson et al. 1994). Most previous field studies lack high spatial resolution in the sampling regime and are focused on broader scale comparisons of fauna in and out of dense beds of carpet-forming suspension feeders (Dittmann 1990; Commito and Boncavage 1989; Ragnarsson and Raffaelli 1999). In such dense bivalve beds, high rates of biodeposition may result in increased microbial activity and reduced conditions in the sediments, leading to benthic communities characterized by low macrofaunal diversity and dominated by opportunistic species such as capitellids and oligochaetes (Commito and Boncavage 1989; Dittmann 1990; Kroencke 1996). Where patches of suspension feeders are less dense, as in this study, they appear to play an important role in promoting macrofaunal diversity.

Through its modification of the habitat, *Atrina* may affect a wide variety of resources such as living space, food, and refuge. Previous studies on *Atrina*-macrofauna interactions (e.g., Cummings et al. 1998, 2001; Thrush et al. in press) have not demonstrated such unequivocal results. However, these studies were conducted over coarser scales compared to this high-resolution study; even more importantly, they were designed to encompass maximum heterogeneity within the bed, rather than target specific locations within bivalve beds, and did not link rates of biodeposition to benthic community structure. Although the interacting effects of habitat structure and deposition of sediments and biodeposits appear to be the ultimate factors, a variety of proximate factors may produce the observed faunal distributions. Both active and passive responses of larvae, juveniles, and adults involving increased recruitment as well as differential survival will be important. For example, passive settlement of larvae and dispersing juveniles and adults is predicted to increase around structures (e.g., Eckman 1990), and active recruitment is further facilitated by the enhanced food supply (e.g., Snelgrove et al. 1992). Faunal distributions could hence be affected by both active habitat selection and by the same extrinsic hydrodynamic processes that control the distribution of food. Differential rates of population growth and survival close to *Atrina* and in bare patches will obviously be affected by differences in food supply; however, other factors, such as predation, could also be important. In general, predation pressure decreases with increasing structural complexity, and hence, some of the higher abundances recorded close to *Atrina* might be due to refuge from predation by epifaunal predators. However, Luckenbach (1987) demonstrated higher abundances of infaunal predators and decreased survival of recently settled bivalves around *Diopatra* tubes, highlighting the importance of complex interactions between biogenic structures and predation in affecting early recruitment.

Our sampling strategy enabled us to identify the potential role of *Atrina* in affecting food resources and small-scale variation in macrobenthic assemblages. It is, however, important to acknowledge that rates of deposition, and hence the strength of the *Atrina*-macrofauna interaction, may vary between sites and between *Atrina* and bare patches over time

in response to varying background conditions (e.g., tides or seasons). The consistency of patterns observed at all our sites, which encompassed a range of environmental conditions, does increase the generality of our findings. Nevertheless, the temporal consistency in patterns of deposition and relative food supply, as well as the relative contribution of the mechanisms discussed above, remains unclear and warrants further work.

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