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ECOSYSTEMS

Changes in Ecosystem Function Across Sedimentary Gradients in Estuaries

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ABSTRACT

The input of terrestrial silt and clay (hereafter mud) into coastal environments can alter sediment grain size distribution affecting the structure and functioning of benthic communities. The relationship between sediment mud content and macrofaunal community structure has been well documented, but not the effects on ecosystem function. In 143 plots from the mid-intertidal sites in 9 estuaries, we measured sediment properties, macrofaunal community composition and fluxes of O_2 and NH_4^+ across the sediment–water interface to derive process-based measures of ecosystem function across the sand–mud gradient. We observed reductions in measures of macrofaunal diversity and decreases in the maximum density of key bioturbating bivalves (*Austrovenus stutchburyi* and *Macomona liliana*) with increased mud content. Concurrently, the maximum rates of sediment oxygen consumption (SOC), NH_4^+ efflux (NH_4^+) and biomass standardized gross primary production ($GPP_{Chl\text{-}a}$) also decreased with increasing mud content. Environmental predictors explained 34–39% ($P = 0.005$–0.01) of the total variation in ecosystem function in distance-based linear models. After partitioning out the effect of mud, *A. stutchburyi* abundance was positively correlated and explained 25 and 23% ($P = 0.0001$) of the variation of SOC and NH_4^+, respectively. Also, mud content (negatively correlated) and temperature (positively correlated) explained 26% of variability in $GPP_{Chl\text{-}a}$ ($P = 0.0001$). Our results highlight the importance of increased mud content and the associated reduction in the abundance of strongly interacting key species on the loss of ecosystem function in intertidal sand flats.

Key words: Bivalves; Sand flats; Key species; Nutrients fluxes; Primary production; Mud content; Factor ceiling; New Zealand.

INTRODUCTION

Anthropogenic alteration of marine ecosystems is projected to have severe consequences for ecosystem functions that humans depend upon, such as primary productivity and biogeochemical cycling (Vitousek and others 1997; MEA 2003; Worm and others 2006). Our ability to predict the long-term ramifications of these changes is limited and the complexity of the processes that deliver these functions can often produce unanticipated results

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(Doak and others 2008). Predictive ability is further hindered by the spatial extent and comparatively long time scale of change associated with major stressors (for example, climate change, ocean acidification, coastal eutrophication), making it difficult to directly extrapolate from small-scale experimental studies. However, analyzing changes in ecosystem function across existing environmental gradients may provide useful insights into the future consequences of environmental change (that is, by inferring future temporal change from existing spatial gradients; Pickett 1989). Estuarine ecosystems exhibit a variety of environmental gradients and are also subjected to a wide range of natural and anthropogenic stressors (Levin and others 2001; Airoldi and Beck 2007). Thus, estuaries are ideal for gradient-based analyses and are likely to show large shifts in function across major gradients.

Elevated sediment runoff as a consequence of change in land-use practices is a major stressor in estuarine ecosystems that are coupled to changes in storm frequency and rainfall intensity (Thrush and others 2004). Increased deposition of terrigenous sediments that contain high proportions of silt and clay (fine particles <63 μm in diameter, hereafter referred to as mud) can cause substantial shifts in grain size distribution, making sandy estuarine sediments muddier (van Rijn 1993). Sampling across sand–mud gradients in estuaries has established that even relatively small increases in mud content can affect the maximum density of a species and cause an overall decrease in species richness (Thrush and others 2003; Anderson 2008). However, it is not clear how these changes will affect the process-based measures of ecosystem function. Given that the benthic macrofauna plays a key role in estuarine nutrient cycling (for example, Henriksen and others 1983; Magni and others 2000; Welsh 2003), primary production [via bioturbation, NH_4^+ excretion and nutrient regeneration (for example, Marinelli and Williams 2003; Lohrer and others 2004)], regulating phytoplankton biomass (for example Cloern 1982; Newell 2004) and as a source of prey for higher trophic levels (for example, Thrush and others 1994; Kraan and others 2009), shifts in macrofaunal diversity are likely to have broad consequences for the entire system. We investigated relationships between macrofaunal diversity and ecosystem function (community metabolism, nutrient regeneration and photosynthetic efficiency by microphytobenthos) across a gradient of increasing mud content on New Zealand intertidal flats. We compiled data from multiple independent studies, which were collected using identical methods, providing comparable data from a broad range of soft-sediment habitat types. Our aim was to determine how much of the variation in ecosystem function could be explained by changes in biotic and abiotic variables (sediment properties, climate) and to provide some indication of the broad-scale effects of increasing inputs of terrigenous sediments.

A growing number of observational studies reveal the significance of biodiversity for ecosystem functioning across broad-spatial scales and how these relationships change along environmental gradients (for example, Hiddink and others 2009; Leduc and others 2012). In many of these studies, biodiversity is quantified as species richness, despite a wide range of other community measures that could equally or possibly better describe the effects of the biota on ecosystem function (Bengtsson 1998). In this study, we considered multiple measures of biodiversity including the abundance of two ecologically important infaunal bivalve species: *Austrovenus stutchburyi*, a shallow burrowing suspension feeder, and *Macomona liliana*, a deeper dwelling surface-deposit feeder. Bioturbating species are pervasive in soft-sediment ecosystems and have a profound influence on sedimentary structure (for example, increasing sediment permeability and subducting organic material) (Boudreau 1998). Through these mechanisms, large bioturbators enhance ecosystem functioning (Lohrer and others 2004). Experimental studies have consistently demonstrated the positive effects of *A. stutchburyi* and *M. liliana* on nutrient regeneration and the facilitation of primary productivity by microphytobenthos (Lelieveld and others 2004; Thrush and others 2006; Sandwell and others 2009; Woodin and others 2010; Jones and others 2011). These relationships have not yet been quantified at larger scales, but we anticipated decreased abundances of these key species coincident with increased mud content (Thrush and others 2003; Anderson 2008) would cause a reduction in ecosystem function disproportionate to other biodiversity measures.

In addition to any species-mediated effects on ecosystem function, changes in grain size, especially at the sediment–water interface, will also directly influence ecosystem processes. For example, increasing mud content will affect the permeability of the sediments, light penetration depth (Billerbeck and others 2007) and rates of solute exchange (Marinelli and others 1998; Ehrenhauss and others 2004) and sediment transport (Morris and Howarth 1998). We investigated the relative importance of biotic and abiotic variables contributing to variation in ecosystem function using distance-based linear models (DISTLM) (Anderson and others 2008). The identification of variables strongly related to function will be important for the assessment and maintenance of ecosystem functioning in the face of elevated sediment runoff.

The complexity of ecological interaction networks that constitute ecosystem function is eroded by anthropogenic modification of the physical habitat and the reduction in density and elimination of species, resulting in lower frequency and magnitude of species–environment interactions (McCauley and others 2012; Thrush and others 2012). Because the extent of ecological functioning is dependent on multiple factors, the effects of increased stress along an environmental gradient are likely to be reflected in patterns of constrained variation and reduced ecological potential of the system (for example, Thrush and others 2008). In this context, we predict that increases in sediment mud content will cause a reduction in the variability of ecosystem function response variables, which will be detectable as declining factor-ceiling response distributions (Thomson and others 1996). Factor-ceiling response distributions relay important information about ecological potential and may be more sensitive in detecting a change in highly variable systems rather than just considering the mean response across environmental gradients (Cade and Noon 2003). We quantified these factor-ceiling trends using quantile regression.

METHODS

Study Sites and Data Compilation

Sites were sampled in the low to mid-intertidal zone in nine estuaries in the North Island of New Zealand (Figure 1). Each site (<500 m^2) contained 3–9 plots, spaced at least 5 m apart. In total, 143 plots were sampled between 2005 and 2011. Data from 123 of the total 143 plots consisting of ambient control plots were collated from several independent experimental studies (Lohrer and others 2010, 2011, 2012; Rodil and others 2011) and additional data were collected from three additional estuaries in April, 2011 to extend the range of sediment mud content (Table 1). We obtained measurements from sediments with mud content (% < 63 μm) ranges that overlapped between sites and estuaries. Consequently, it is unlikely that the effects of mud content on function could be confounded by between-estuary variation in other geomorphological or hydrodynamic conditions. At the plot scale, mud content varied from 0.3 to 29.7% and site water temperatures ranged from 14°C in July to 26°C in February (Table 1).

Ecosystem Properties and Function

Measures of ecosystem function were derived from solute fluxes in paired light and dark benthic chambers, because they are directly related to the transfer of energy and material between different abiotic and biotic components of the ecosystem. Measurements of sediment oxygen consumption (SOC) reflect rates of community metabolism and chemical oxidation processes in the sediment. The efflux of nutrients from sediment to the water column (hereafter ''nutrient regeneration'') is important for primary production and is a useful indicator of the self-sustainability of a system (for example, Danovaro and others 2008). Sediment microphytobenthos (MPB) can contribute up to 83% of primary productivity in estuaries (MacIntyre and others 1996), and because mud content is likely to impact the ability of MPB in the system to utilize resources (for example, light and nutrients), we quantified the biomass specific rates of gross primary production ($\mathrm{GPP}_{\mathrm{Chl}\text{-}a}$) as an estimate of photosynthetic efficiency.

Light and dark incubation chambers (area = 0.016 m^2, vol. = 0.85 l) were deployed to quantify the effects of sediment mud content and other environmental variables on solute fluxes at the sediment–water interface in the presence and absence of photosynthetic activity by MPB. The same methodology (see Lohrer and others 2010, 2011, 2012; Rodil and others 2011) has been adopted in all studies removing a potentially important source of variability from the amalgamated data set. Briefly, sampling occurred on dates with a mid-day high tide (1100–1400 h) to ensure an adequate incubation period (ca. 4 h) under generally sunny, calm conditions. Within a plot, 1–3 pairs of light and dark chambers were deployed with 0.3–0.5 m between pairs. Solute fluxes were calculated from the initial and final concentrations in chamber water samples and standardized by the elapsed time of incubation. To account for any water column effects on solute fluxes, ambient seawater was incubated in paired light and dark bottles (n = 3 per site) for the duration of the chamber incubation. Water column affects accounted for 0–3% of the measured chamber fluxes; thus, it was not necessary to correct chamber flux values prior to analysis. Dissolved oxygen concentrations of chamber-incubated samples and ambient seawater were measured using an optical D.O. probe (RDO, In-Situ Incorporated, Fort Collins, Colorado 80524, USA). Sample water was filtered

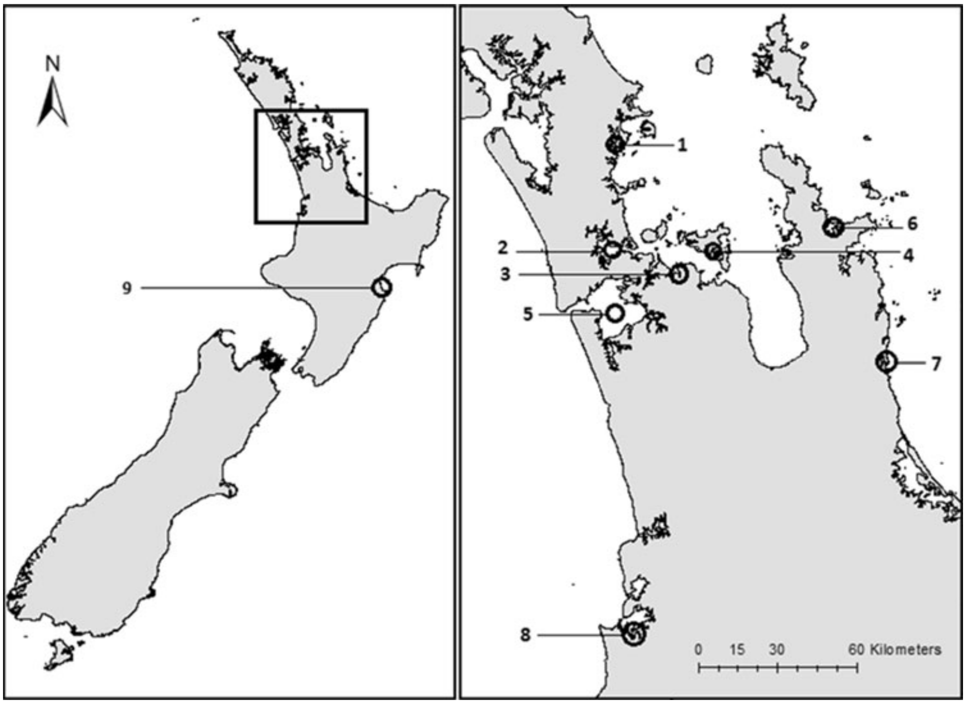

Figure 1. **A** Location of main sampling region and the Ahuriri Estuary (9). **B** Locations of remaining estuaries. The estuary reference numbers are given in Table 1.

through a Whatman GF/C grade filter (2.4 cm diameter, 1.2 µm pore size) in a Swinnex filter holder and stored for nutrient analysis. HOBO data loggers were deployed at four locations per site to quantify variability in ambient water temperature (T_w) and light (L_w) that can strongly affect sediment oxygen and nutrient exchange by altering the rates of biological and physico-chemical processes. To supplement the HOBO data, climate data [air temperature (T_a) and irradiance (L_a)] were acquired from the National Climate Database (CliFlo, http://cliflo.niwa.co.nz/).

In each plot, faunal and sediment properties were measured next to benthic chambers and analyzed using consistent methodologies (see Lohrer and others 2010 for details). One macrofauna core (13 cm dia., 15 cm depth) was collected within a 0.5-m distance of the benthic chambers. Since the variability in the abundances of common macrofauna is low at the scale (plot scale) of our measurements (Thrush and others 1989; Hewitt and others 1996), we considered our estimated values of macrofauna variables to be representative of sediments underneath benthic chambers. Four surface sediment cores (2.4 cm dia., 2 cm depth) were sampled from random positions within the plot to account for spatial variation in sediment properties. From each macrofauna core, we identified and counted all organisms retained on a 500-µm sieve. In subsequent analyses, we considered separately the abundances of two key bivalve species, *Austrovenus stutchburyi* (suspension feeder) and *Macomona liliana* (deposit feeder). For the wider macrofauna community, we considered univariate measures of diversity: number of individuals excluding the two key species mentioned above (*N*), taxonomic richness (Taxa) and Shannon-Wiener diversity (H′). The four surface sediment cores were amalgamated for the analysis of grain size [median grain size, MGS; percentage mud content (Gatehouse 1971)], organic matter content (OC; by loss on ignition (Mook and Hoskin 1982)) and chlorophyll-*a* content (Chl-*a*) as a proxy of MPB biomass (Sartory 1982). We also determined phaeopigment concentration (Phaeo) to distinguish between viable chlorophyll *a* and refractory/degraded pigment biomass. Inorganic nutrient (ammonium, NH_4^+; nitrate plus nitrite, NO_X and phosphate, PO_4^{3-}) concentrations were measured on a Lachat QuickChem 8000 Series FIA+ (Zellweger Analytics Inc. Milwaukee, Wisconsin, 53218, USA) using the Lachat standard operating procedures for flow injection auto-analysis. The measured changes in solute concentrations during the incubation period were much larger than the detection limits; therefore, the derived fluxes were often several orders of magnitude above the minimum detectable flux (O_2 = 3.77 µmol O_2 m^{-2} h^{-1}, NH_4^+ = 0.78 µmol NH_4^+ m^{-2} h^{-1}).

Data Analysis

SOC was determined from dark chamber oxygen fluxes. Dark chamber ammonium fluxes (NH_4^+)

Table 1. Sampling Location and Date, and Environmental Details

Ref #	Estuary	Site location		Sample date	Plots (n)	Mud content (%)	L_a (MJ m^{-2} h^{-1})	T_a (°C)	T_w (°C)
1	Mahurangi	36°28.72′S	174°42.86′E	04/02/2005[1]	3	7.8–11.5	2.91	24.4	26.0
				07/06/2005[1]	3	7.8–11.8	1.94	13.4	14.0
				09/02/2006[1]	3	6.0–10.3	1.82	18.3	24.0
		36°28.61′S	174°41.90′E	04/02/2005[1]	3	1.4–1.9	2.91	24.4	26.0
				07/06/2005[1]	3	9.9–13.9	1.94	13.4	14.0
				09/02/2006[1]	3	7.6–19.9	1.82	18.3	24.0
		36°28.46′S	174°43.80′E	04/02/2005[1]	3	15.3–23.0	2.91	24.4	26.0
				07/06/2005[1]	3	12.0 –17.2	1.94	13.4	14.0
				09/02/2006[1]	3	8.4–12.5	1.82	18.3	24.0
2	Waitemata	36°51.37′S	174°39.67′E	09/03/2006[2]	3	3.8–5.4	1.74	17.9	21.7
				10/03/2006[2]	3	4.8-6.2	2.53	18.3	21.5
				24/04/2007[3]	9	4.1–10.3	1.64	17.7	23.2
		36°51.44′S	174°47.60′E	26/04/2007[3]	9	3.9-6.8	1.55	19.8	24.3
		36°54.06′S	174°47.60′E	27/04/2007[3]	9	10.3–17.3	1.63	18.8	26.1
		36°50.88′S	174°42.86′E	12/05/2008[3]	9	4.9	1.41	13.7	16.7
3	Whitford	36°54.47′S	174°58.87′E	13/05/2008[3]	9	5.4	1.82	13.5	15.8
		36°54.49′S	174°59.37′E	11/04/2011†	8	3.2–29.7	1.42	19.4	24.1
4	Waiheke Island	36°50.27′S	174°07.98′E	07/03/2006[2]	3	7.0–9.4	0.58	18.6	23.2
				08/03/2006[2]	3	6.3–8.0	1.38	19.4	23.8
5	Manukau	37°00.22′S	174°34.17′E	07/05/2008[3]	9	7.1	1.60	12.8	17.0
		36°55.74′ S	174°45.66′E	08/05/2008[3]	9	15.7	1.62	14.7	15.8
6	Whangapoua	36°44.30′S	175°37.28′E	28/11/2006[4]	4	1.0–2.6	2.15	17.9	24.7
		36°44.20′S	175°37.22′E	28/11/2006[4]	4	0.5–0.8	2.15	17.9	24.7
		36°44.26′S	175°37.43′E	28/11/2006[4]	4	0.3–0.6	2.15	17.9	24.7
7	Whangamata	37°10.63′S	175°51.68′E	13/04/2011[5]	8	12.6–25.0	1.51	18.8	25.6
8	Kawhia	38°08.06′S	174°49.20′E	08/04/2011[5]	8	13.7–22.8	2.18	16.6	19.6
9	Ahuriri	39°29.27′S	176°53.06′E	26/04/2010[6]	9	12.1–19.7	0.87	21.7	19.3

Ref # gives the location of the estuary in Figure 1; L_a surface light intensity (MJ m^{-2} h^{-1}); T_a and T_w denotes, respectively, land-surface air and ambient water temperature (°C); data were collated from various studies but using identical methodologies.

[1] *Lohrer and others 2010.*

[2] *Lohrer and others 2011.*

[3] *Lohrer and others 2012.*

[4] *Rodil and others 2011.*

[5] *Present study.*

[6] *Unpublished.*

were used as a measure of nutrient regeneration rates [in the absence of uptake by photosynthesizing MPB that would occur in light chambers (Thornton and others 1999)]. Ammonium comprised up to 99% of the total dissolved inorganic nitrogen flux and is the form of nitrogen most readily available to primary producers. PO_4^{3-} and NO_X were not considered because they did not generate significant relationships with predictor variables and concentrations were often near detection limits. Rates of gross primary production per unit of chl-*a* were estimated from differences in paired light and dark chamber O_2 fluxes, providing a measure of photosynthetic efficiency. In plots containing more than one pair of light and dark chambers, we averaged the fluxes from replicate chambers.

Bivariate scatterplots of almost all response variables versus sediment mud content revealed high variability and distributions indicative of factor ceilings (Thomson and others 1996; Thrush and others 2012). We therefore quantified factor-ceiling trends using quantile regression models fitted with linear, exponential and unimodal functions, computed in the Quantreg package (Koenker 2012) in R (R version 2.15, 2012). Conservative estimates of the response maxima were determined at the 90th percentile ($\tau = 0.9$) and the best fitting models were chosen based on statistical significance (*P* values).

To identify the biotic and abiotic predictor variables contributing to variation in ecosystem function, DISTLM were performed using the PERMANOVA add-on for PRIMER v6 (Anderson and others 2008). DISTLM performs a partitioning in the variation in data matrices similar to regression, but it generates P values by a permutation routine (Anderson and others 2008). Initially, models were run to identify significant predictors of ecosystem function when fitted individually (marginal test) and then sequentially using the step-wise selection procedure and R^2 criteria (step-wise tests). Biodiversity effects covary with many abiotic factors associated with environmental gradients. Therefore, we investigated the relationships between the best predictor and ecosystem function response variables after accounting for environmental variables by fitting first mud content (sequential I) and in a separate test all environmental predictor variables (sequential II) using the specified selection procedure. Model parsimony was assessed by repeating the tests using Akaike information criterion. Similarity matrices were constructed using Euclidean distance and P values were obtained for predictor variables by 9,999 permutations. DISTLM is a ''semi-parametric'' analysis and does not assume normality or homogeneity of variances, but predictor variables were transformed when necessary to improve the linear fit of the data. Non-significant predictor variables were ruled out from the analyses. To avoid multicollinearity, significant co-linear relationships were identified between predictor variables (Pearson's $r > 0.7$) and the redundant predictor variables (explaining the least proportion of the variation in the model) were omitted.

RESULTS

Sediment—Macrofauna Relationships

Sediments at the majority of sites were classed as fine sands with median grain size ranging between 94 and 232 µm and mud content from around 0 to 30%. All plot-specific information can be found in Supplementary Appendix 1. Each 5% mud content range (for example, 0–5%) comprised information from 4 to 10 sites located in 4–6 estuaries indicating good interspersion of the data. The only exception to this was in the 25–30% mud content range which contained data from two sites in one estuary. Increases in sediment mud content were concomitant with changes in other sediment properties: decreasing median grain size and increasing organic content and phaeopigment concentration (Table 2). The key species *A. stutchburyi* and *M. liliana* were found at all sites, identified in greater than 82% of the plots and densities ranged between 0–51 and 0–15 ind. core^{-1} respectively. In all cases, these two bivalve species represented the dominant macrofauna in terms of size and biomass.

All measures of macrofaunal diversity and key species abundances were negatively correlated with mud content (Figure 2; Table 2). Factor-ceiling responses detected at the 90th percentile ($\tau = 0.9$) for taxonomic richness and key species abundances declined linearly, while community abundance declined exponentially (Figure 2). The decline in all measures of macrofaunal diversity with increased mud content was substantial. For example, maximum taxonomic richness decreased from 22 to 11 taxa between 0 and 30% mud (Figure 2A, D). We estimated a 60 and 100% reduction in the maximum abundances of *A. stutchburyi* and *M. liliana*, respectively, across the sedimentary gradient. However, it is apparent that *A. stutchburyi* and *M. liliana* can still persist at high densities (29 and 10 ind. core^{-1}) in sediments with relatively high mud content (16–25% respectively, Figure 2A, B). We did not observe a significant factor-ceiling relationship between mud content and Shannon-Wiener diversity (H′, $P > 0.55$ for the linear model) despite a significant correlation between these factors (Table 2). We found that *A. stutchburyi* abundances displayed particularly strong, positive relationships with macrofaunal community abundance (Pearson's $r = 0.65$; Table 2) and taxonomic richness ($r = 0.50$). However, the correlations between both *A. stutchburyi* and *M. liliana* abundance and MPB biomass were weak ($r < 0.23$).

Ecosystem Function

All measures of ecosystem function were negatively correlated with mud content, showing high variability in sediments with low mud content and a more restricted range of responses in muddier sediments. Significant linear reductions in the maximum rates of SOC (68%; $\tau = 0.9$ $P = 0.001$) and nutrient regeneration (80%; $\tau = 0.9$ $P < 0.001$) were apparent between the ranges of 10 and 30% sediment mud content (Figure 3A, B). The influence of mud content on nutrient regeneration was specific to the response maxima and was not significantly correlated in Pearson's r (Table 2). GPP normalized to chlorophyll-*a* biomass ($\mathrm{GPP}_{\mathrm{Chl}\text{-}a}$) was the most sensitive ecosystem function to increases in mud content. These variables were significantly correlated in Pearson's r ($P < 0.001$, Table 2), and we found a 79% reduction in the maximum rates of $\mathrm{GPP}_{\mathrm{Chl}\text{-}a}$ ($\tau = 0.9$ $P = 0.016$) over the approximately 0–30% change in mud content (Figure 3C).

Table 2. Pearson's Correlation Coefficients (r) Between (a) Environmental Variables and (b) Environmental Variables and Ecosystem Functions

	MGS	Mud	OC	Chl-*a*	Phaeo	T_w	L_a	*N*	Taxa	H′	*A. stu*	*M. lil*
(a)	Environmental variables											
MGS	1.00											
Mud	−0.49***	1.00										
OC	0.01	0.51***	1.00									
Chl-*a*	−0.02	0.02	0.28***	1.00								
Phaeo	0.06	0.44***	0.44***	−0.11	1.00							
T_w	0.18*	0.09	−0.11	0.09	0.35***	1.00						
L_a	0.28**	−0.28**	0.06	0.07	−0.02	0.11	1.00					
Taxa	0.38***	−0.53***	−0.16	0.26**	−0.12	0.05	0.31***	1.00				
N	0.21**	−0.38***	−0.01	0.48***	−0.11	0.07	0.25**	0.75***	1.00			
H′	0.41***	−0.30***	−0.10	0.12	−0.02	−0.08	0.16	0.14	0.62***	1.00		
A. stu	0.32***	−0.23**	−0.01	0.23**	−0.11	0.08	0.14	0.65***	0.50***	0.13	1.00	
M. lil	0.58***	−0.36**	−0.10	0.11	−0.19*	0.08	0.22	0.22**	0.42***	0.47***	0.20*	1.00
(b)	Ecosystem functions (response variables)											
SOC	0.16	−0.23**	0.11	0.35***	0.03	0.22**	0.11	0.51***	0.35***	0.00	0.54***	−0.02
NH_4^+	0.15	−0.08	0.22**	0.28**	0.15	0.06	0.04	0.43***	0.19*	0.14	0.49***	−0.17*
$GPP_{Chl\text{-}a}$	0.18*	−0.39***	−0.42***	n/a	−0.29***	0.37***	0.35***	0.09	0.30***	0.26**	0.07	0.30**

Data from all plots were combined. (a) Environmental variables: MGS = median grain size (μm); Mud = mud content (%); OC = organic content (%); Chl-a = chlorophyll-a biomass (μg dw Chl-a g^{-1} sediment); Phaeo = phaeopigment (μg dw Phaeo g^{-1} sediment); N = macrofaunal abundance (ind. $core^{-1}$) excluding key species; Taxa taxonomic richness and H′ = Shannon-Wiener diversity. A. stu and M. lil are the abundance (ind. $core^{-1}$) of the key species A. stutchburyi and M. liliana, respectively. Climate variables included are L_a = surface irradiance (MJ m^{-2} h^{-1}) and T_w = water temperature (°C). (b) Ecosystem functions: SOC = sediment oxygen consumption (μmol O_2 m^{-2} h^{-1}); NH_4^+ = dark chamber ammonium flux (μmol NH_4^+ m^{-2} h^{-1}); $GPP_{Chl\text{-}a}$ = gross primary production normalized to chlorophyll biomass (μmol O_2 μg g^{-1} dw Chl-a m^{-2} h^{-1}). To improve the normality of the data distribution, arcsine (mud), log (OC, Chl-a and Phaeo) and square-root (N, A. stu and M. lil) transformations were applied.

$* P < 0.05$.

$** P < 0.01$.

$*** P < 0.001$.

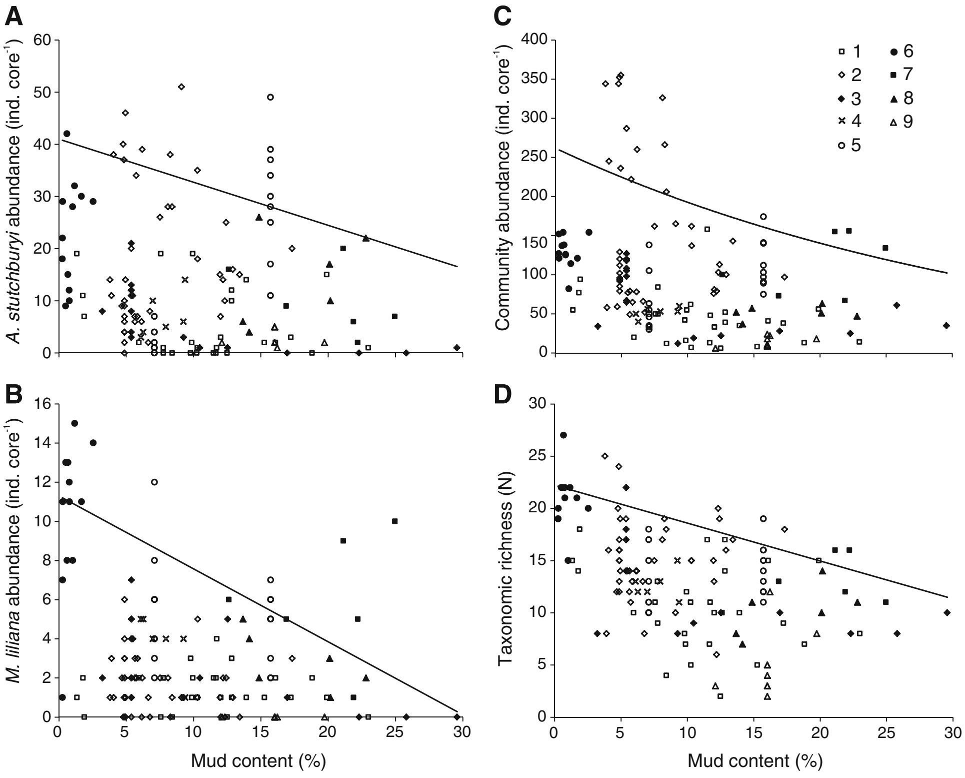

Figure 2. Macrofaunal community parameter estimates as a function of mud content. Regressions fitted at 90th percentile distributions. Slope coefficients (and model) for the 90th percentile are reported for **A** *A. stutchburyi* abundance [0.9, slope (linear) = −0.83, $P = 0.043$], **B** *M. liliana* abundance [0.9, slope (linear) = −0.37, $P = 0.036$], **C** community abundance [0.9, slope (exponential) = −0.03, $P = 0.02$] and **D** taxonomic richness [0.9, slope (linear) = −0.36, $P < 0.001$]. *Symbols* indicate data from different estuaries, the reference numbers are given in Table 1.

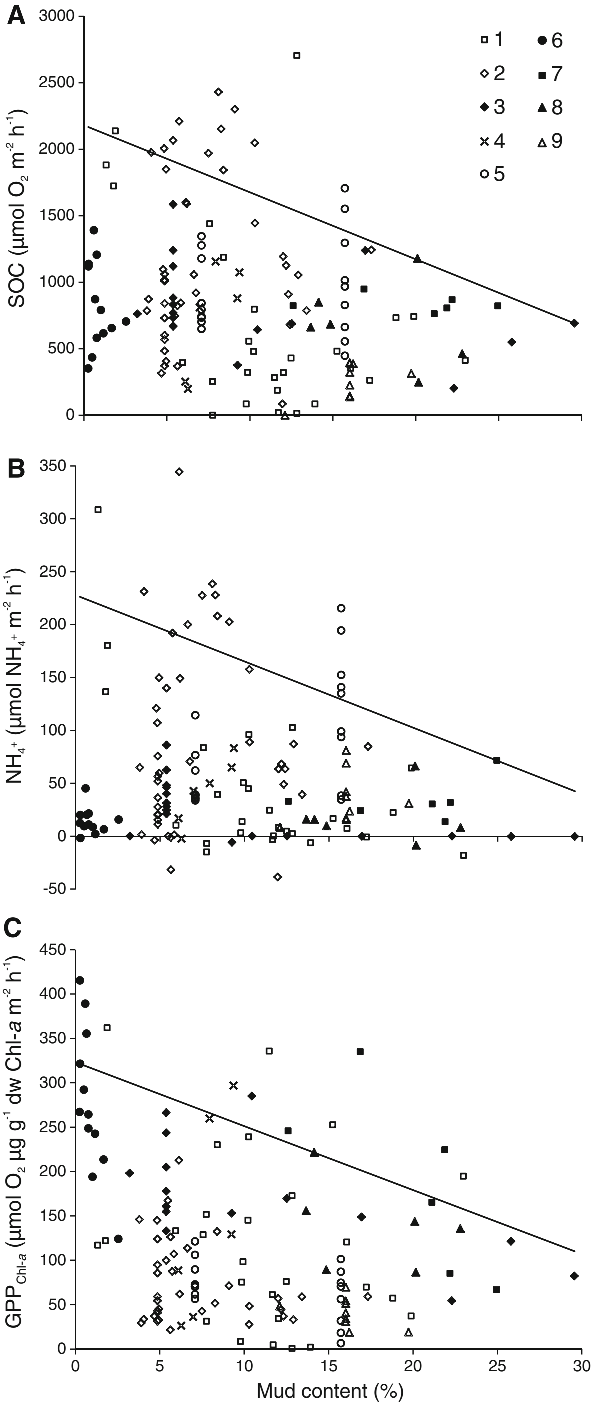

Figure 3. Ecosystem function rate estimates as a function of mud content. Regressions fitted at 90th percentile distributions. Slope coefficients (and model) for the 90th percentile are reported for **A** sediment oxygen consumption [0.9, slope (linear) = −50.32, $P = 0.001$], **B** nutrient regeneration [0.9, slope (linear) = −6.27, $P < 0.001$] and **C** biomass normalized gross primary production [0.9, slope (linear) = −7.20, $P = 0.016$]. *Symbols* indicate data from different estuaries, the reference numbers are given in Table 1.

DISTLM were run to identify the best predictor variables contributing to ecosystem function. When fitted individually in the marginal tests, predictor variables explained between 3 and 29% of the variation in SOC and nutrient regeneration. *A. stutchburyi* and community abundance (N) explained the highest proportion of variation for both response variables (Table 3). Predictor variables were then fitted sequentially in step-wise tests. Predictor variables for SOC (N, T_w and Chl-a) and nutrient regeneration (*M. liliana*, N and MGS) were retained, but each explained a very low proportion of the variance (<7%) when fitted sequentially after *A. stutchburyi* in the most parsimonious step-wise models. The proportion of variance explained by *A. stutchburyi* abundance for both of these response variables was only marginally lower after accounting for mud content as a covariate (sequential I). In a separate sequential test, the relationship between *A. stutchburyi* abundance + N (grouped due to large similarity in explained variance) and ecosystem function was tested after first fitting all significant environmental predictor variables (sequential II, Table 3). Here, *A. stutchburyi* + N still explained a higher proportion of variation than the sum of all other environmental predictor variables. Other measures of macrofaunal diversity (H′ and Taxa) were less effective predictors of ecosystem function. Taxa displayed strong covariation with N and was excluded as a predictor variable from explanatory models of both SOC and nutrient regeneration. While mud content tends to constrain the maximum rates and variation in the range of response, it does not appear to drive changes in the central tendency for SOC or nutrient regeneration. However, it is important to acknowledge that the variables that most effectively explain variability in these functions (that is, *A. stutchburyi*, *M. liliana*, N and MGS) are also significantly influenced by mud content (Figure 2; Table 2).

DISTLM revealed that mud content was the most effective predictor of $GPP_{Chl\text{-}a}$, explaining 15% of the total variation in marginal tests. Climatic variables T_w and L_a, respectively, explained 13 and 12% of the variability in $GPP_{Chl\text{-}a}$. While *M. liliana* was also significantly related to $GPP_{Chl\text{-}a}$, its contribution was small (3%) when fitted after mud content and climate variables in step-wise tests (Table 3). Both results from the quantile regression and DISTLM suggest that mud content plays a more direct role in determining $GPP_{Chl\text{-}a}$, which is not consistent with its effects on SOC and nutrient regeneration. However, the proportion of variance in $GPP_{Chl\text{-}a}$ explained by mud content was markedly lower after

Table 3. Distance-based Linear Model Results Between Environmental Predictors and Ecosystem Functions

Ecosystem function	Predictor	*P*	Prop	Cumul. R^2	res. *df*
SOC					
Marginal	*A. stu*	0.0001	0.29		
	N	0.0001	0.26		
	Chl-*a*	0.0001	0.12		
	T_w	0.01	0.04		
Step-wise	*A. stu*	0.0001	0.29	0.29	141
	N	0.0001	0.07	0.35	140
	T_w	0.02	0.03	0.38	139
	Chl-*a*	0.06	0.02	0.39	138
Sequential (I)	Mud	0.005	0.05	0.05	141
	A. stu	0.0001	0.25	0.30	140
Sequential (II)	All env	0.0001	0.18	0.18	138
	A. stu + N	0.0001	0.19	0.37	137
NH_4^+					
Marginal	*A. stu*	0.0001	0.24		
	N	0.0001	0.18		
	MGS	0.05	0.03		
	M. lil	0.05	0.03		
Step-wise	*A. stu*	0.0001	0.24	0.22	141
	M. lil	0.0003	0.07	0.31	140
	N	0.002	0.05	0.36	139
	MGS	0.005	0.04	0.39	138
Sequential (I)	Mud	0.31	0.01	0.01	141
	A. stu	0.0001	0.23	0.24	140
Sequential (II)	All env	0.0001	0.20	0.20	138
	A. stu + N	0.0001	0.22	0.42	137
$GPP_{Chl\text{-}a}$					
Marginal	Mud	0.0001	0.15		
	T_w	0.0001	0.13		
	L_a	0.0001	0.12		
	M. lil	0.0002	0.09		
Step-wise	Mud	0.0001	0.15	0.15	141
	T_w	0.0001	0.11	0.26	140
	L_a	0.004	0.05	0.30	139
	M. lil	0.01	0.03	0.34	138
Sequential (II)	All env	0.0001	0.31	0.31	138
	Mud	0.008	0.04	0.35	137

Data from all plots combined (n = 143). Marginal tests show the proportion of variation explained by predictor variables fitted individually. Step-wise tests (using step-wise selection procedure and R^2 selection criteria) determine the variance explained by predictor variables when fitted sequentially. The strongest predictor variables were tested after fitting mud content as a covariate (sequential I) and then after first fitting all significant environmental predictor variables shown in Table 2 (sequential II). Resemblance matrices generated by Euclidian-distances of the raw and transformed data. Environmental variables: MGS = median grain size (µm); Mud = mud content (%); OC = organic content (%); L_a = surface irradiance (MJ m^{-2} h^{-1}); T_w = ambient water temperature (°C); Chl-a = chlorophyll-a biomass (µg dw Chl-a g^{-1} sediment). Macrofauna biodiversity indices: N = community abundance excluding key species (ind. $core^{-1}$); A. stu = A. stutchburyi abundance (ind. $core^{-1}$); M. lil = M. liliana abundance (ind. $core^{-1}$). Ecosystem functions: SOC = sediment oxygen consumption (µmol O_2 m^{-2} h^{-1}); NH_4^+ = nutrient regeneration (µmol NH_4^+ m^{-2} h^{-1}); $GPP_{Chl\text{-}a}$ = gross primary production normalized to chlorophyll biomass (µmol O_2 µg g^{-1} dw Chl-a m^{-2} h^{-1}).

accounting for other significant environmental predictors: climate, macrofaunal diversity and sediment properties in the second set of sequential tests. Therefore, the effects of mud content are also related to the effects of other abiotic and biological variables. Strong co-variation was identified between predictor variables T_w and T_a, and between *N* and Taxa. The lesser predictors of $GPP_{Chl\text{-}a}$ (T_a and Taxa) were excluded from the models. There was no correlation between Chl-*a* and mud content (Table 2). However, our data suggest that the capacity for primary productivity was not directly related to autotroph biomass, because the rates of pre-standardized GPP were not significantly related to Chl-*a* (r = 0.12).

DISCUSSION

The muddying of estuarine sediments as a consequence of land-use change in coastal catchments poses a threat to the biodiversity and functioning of coastal ecosystems (Thrush and others 2004). Under a regime of increasing sedimentation, the areal extent of mud flats may expand at the expense of sand flats, and the mud content of sandy habitats may increase. However, it may take many years for such changes to become apparent, hindering our ability to document and quantify the threat. One way forward is to sample across existing spatial gradients (that is, both muddy to sandy habitats) to gain insights into the trends that may occur over time (space-for-time substitution; Pickett 1989).

All of the macrofaunal variables measured (abundance of *A. stutchburyi* and *M. liliana*, community abundance, taxonomic richness and diversity) declined with increasing sediment mud content, consistent with the findings of previous studies (Thrush and others 2003; Anderson 2008). The predominant form of response was a factor-ceiling relationship: sediments with less mud had a greater range of variation and higher maximum values than sediments with more mud. The process-based variables indicative of ecological functioning (SOC, nutrient regeneration and $\mathrm{GPP}_{\mathrm{Chl}\text{-}a}$) also exhibited factor-ceiling responses. Large values suggestive of high levels of ecological intactness and functioning were rarely observed in sediments with high mud content. Fewer data were available for sediments containing high ranges of mud content (25–30%), but this sampling limitation did not significantly affect response variation patterns. Statistical analyses were repeated for a subset of the data containing a range of 0–25% mud content and only marginal differences in statistical results were noted. The patterns of response in the process-based variables were explained by both biotic and abiotic factors, with SOC and nutrient regeneration explained most effectively by *A. stutchburyi* abundance, and with $\mathrm{GPP}_{Chl\text{-}a}$ explained by mud content and climatic factors.

Although the effects of mud content were most apparent in terms of response maxima (particularly for individual species densities *A. stutchburyi* and *M. liliana*), they were also detectable using conventional correlation models. Thrush and others (2003) pointed out that these trends in species densities across gradients have important implications for ecosystem functions supported by these communities. Relationships between individual species and ecosystem functions (for example, nutrient regeneration) are often density dependent, where higher rates of function correspond with higher macrofaunal densities (Marinelli and Williams 2003; Sandwell and others 2009). The implication is that transformations of high-density patches to low-density patches as a result of anthropogenic stress can severely reduce the functional contributions of these populations.

While biodiversity declines in response to increasing mud content have been repeatedly demonstrated (Thrush and others 2003; Anderson 2008), and links to functioning have been inferred from changes in the densities of key species (Marinelli and Williams 2003; Lohrer and others 2004; Thrush and others 2006; Sandwell and others 2009; Jones and others 2011), this is the first time that declines in functioning in response to mud have been explicitly documented in the field across a multi-estuary sand-to-mud gradient. Relationships between measures of macrofaunal diversity and ecosystem function remained robust after accounting for other significant environmental predictor variables and despite the sampling of macrofauna outside the area of the incubation chambers that likely added further unexplained variation. The effects of anthropogenic stressors on biodiversity and ecosystem function are often inferred from reductions in species richness. Here, although taxonomic richness was inversely related to mud content, rates of ecosystem function responses were more strongly related to the abundances of two key species. The influence of *A. stutchburyi* and *M. liliana* to solute exchange may, on one hand, be attributable to their size dominance in the macrofaunal community, as metabolic activity (respiration and NH_4^+ excretion) is fundamentally related to the body size of the organism (Banse 1982; Brown and others 2004). Moreover, soft-sediment habitats are complex interactive systems. Bioturbation by these species can enhance nutrient remineralization rates by the microbial community by increasing sediment permeability, oxygen availability and by concentrating and subducting organic material (Henriksen and others 1983; Lohrer and others 2004; Mermillod-Blondin and others 2004). Thus, by modifying sediment properties and modulating resources available to other organisms, the key species can also influence functioning via other biological components of the system.

Explanatory models for $\mathrm{GPP}_{\mathrm{Chl}\text{-}a}$ revealed strong overlapping effects of mud content with other significant environmental predictor variables. Thus, the limiting role of mud content on benthic ecological functioning is more identifiable as a structuring factor within a complex interaction network rather than a simple cause-and-effect process. As such, there are biogeochemical links between almost all variables measured in this study; the remineralization of organic matter results in the regeneration of inorganic nutrients that can be taken up by MPB. MPB in turn are fed upon by many types of macrofauna, which defecate organic-rich biodeposits and excrete ammonium nitrogen (for example, Welsh 2003; Lohrer and others 2004). Thus, the patterns of variability that we observed and the types of analyses we used were consistent with our conceptual understanding of the system. In this study, the linkages between macrofaunal and key species abundances and $GPP_{Chl\text{-}a}$ were weak. This is not surprising in view of recent experimental studies showing that the performance of bioturbators and their contribution to sediment functioning vary with habitat type (Jones and others 2011; Needham and others 2011). Moreover, the role of *A. stutchburyi* in facilitating MPB productivity may be restricted to sandy, more permeable sediments (Jones and others 2011). In muddier sediments, the reduction in grain size (and permeability), concurrently lower light, oxygen penetration depth and rates of nutrient transport place a large constraint on $GPP_{Chl\text{-}a}$. Taken together, it is clear that such biogeochemical linkages are weaker in muddier sediments because key species become less abundant and MPB are less able to efficiently utilize internally regenerated nutrients.

This study provides compelling evidence that increases in sediment mud content could threaten the ecological functioning of shallow soft-sediment habitats. Changes in functioning were linked to changes in sediment properties, altered community structure and loss of key components of biodiversity. Reduced densities of strongly interacting key species will tend to reduce the biocomplexity of these communities and the interaction networks that define them (McCauley and others 2012; Thrush and others 2012). This concept of a ''simplified'' ecosystem architecture in degraded or impacted environments fits the findings of our study, considering the reductions in multiple elements of biodiversity and the physical constraints imposed on biogeochemical processes by the muddying of sediments. The reduction of interactions between multiple ecological components is reflected in the variability of ecosystem function that is constrained in sediments with higher mud content. As mud content increases, other environmental variables become less important in explaining the variation in ecosystem function, and the systems become simpler and closer to functional extinction (sensu Dayton and others 1998).

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