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Site-dependent effects of bioturbator–detritus interactions alter soft-sediment ecosystem function

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ABSTRACT: In coastal sediments, macrofauna can trap macrophyte detritus in their burrows, modifying organic matter retention/export. However, the resulting effects on ecosystem function are unclear. We conducted a field experiment to assess how detrital processing by a common bioturbating crab *Austrohelice crassa* influences benthic metabolism, primary production, and ammonium regeneration at a sand and muddy-sand site. Since the functional role of crabs and detrital decay rates vary with mud content, we hypothesised their interactive effects on ecosystem function would also vary. Sixteen cages (0.36 m^2) were established at each intertidal site, and cages were allocated a crab (0 or 35 ind. $cage^{-1}$) and seagrass detritus (0 or 120 g dry weight [DW] $cage^{-1}$) treatment. Ten days later, sediment–water solute fluxes were measured. Treatment effects on ecosystem function were site-specific: detritus stimulated benthic metabolism in muddy-sand (by 12 to 29%, $p = 0.01$), but in sand, effects were dominated by crabs. Metabolism increased by 12 to 21% ($p = 0.04$), of which 24 to 52% could be attributed to crab respiration. Crabs enhanced ammonium regeneration in sand ($p < 0.003$), of which <26% could be attributed to crab excretion, but in muddy-sand, the presence of detritus masked this positive effect (dark ammonium flux, crab × detritus interaction: $p = 0.03$). Crabs and detritus had negative effects on primary production in sand, where crabs reduced primary production by 57% and detritus by 73%. In muddy-sand, variable light conditions made primary production estimates unreliable. Our results emphasise that context is paramount when understanding the effects of reductions in the densities of key species or changes in detrital inputs on soft-sediment ecosystem function.

KEY WORDS: Bioturbation · *Austrohelice crassa* · Detrital decay · Primary production · Nutrient flux · Grapsid · Seagrass · Benthic community metabolism

INTRODUCTION

Anthropogenically driven changes in biodiversity are predicted to have far reaching effects on coastal marine ecosystem function (e.g. productivity and nutrient processing), and the derived ecosystem services that society values (Norkko et al. 2013, Snelgrove et al. 2014). This biodiversity change is of particular concern in coastal soft sediments, where catchment land-use changes and over harvesting have often resulted in the decline of functionally important flora (e.g. seagrass habitat; Inglis 2003, Moore & Short 2006) and fauna (e.g. shellfish; Rothschild et al. 1994, Thrush et al. 2003). In these habitats, complex interactions between organisms and their sedimentary environment regulate important ecosystem functions involving the decomposition of organic matter, and the flux of particles and solutes across the sediment–water interface that support pelagic production (e.g. Thrush et al. 2006, Fanjul et al. 2011, Volkenborn et al. 2012, Norkko et al. 2013, Snelgrove et al. 2014). Since approximately 50% of

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global organic matter remineralisation occurs in coastal benthic habitats (Middelburg et al. 1997), declines in the benthic species that regulate ecosystem functions associated with nutrient cycling are likely to have wider consequences for coastal food webs.

Bioturbating macrofauna oxygenate seabed sediments by mixing and actively ventilating them, altering sediment biogeochemistry (e.g. Williamson et al. 1999, Welsh 2003, Vopel et al. 2003, Volkenborn et al. 2010, 2012). By altering redox layer distribution, bioturbators can speed up microbial processes associated with nutrient regeneration (i.e. faster remineralisation processes in oxic layers; Aller 1988, Kristensen et al. 1995, Kristensen 2000). Bioturbators also increase the transport of remineralised nutrients between the sediment and overlying water, through processes including burrow irrigation, pore water advection, and sediment particle reworking, as without them solute transport is largely limited to diffusion across the benthic boundary layer (reviewed in Kristensen et al. 2012). Furthermore, fauna can directly influence sediment–water nutrient fluxes through excretion, increasing nutrient availability at the sediment–water interface (Welsh 2003, Welsh et al. 2015, Woodin et al. 2016). Accordingly, bioturbators make a positive contribution to benthic and water column primary production in the photic zone by releasing biologically available inorganic nitrogen from seabed sediments (e.g. measured as an efflux of nitrogen across the sediment–water interface; Kristensen & Hansen 1999, Lohrer et al. 2004, Fanjul et al. 2008, Sandwell et al. 2009, Fanjul et al. 2011, Needham et al. 2011, Norkko et al. 2013).

Adding to the complexity of organism–sediment interactions, bioturbators also facilitate vertical movement of organic matter in the sediment column, as fauna-induced sediment mixing either buries or uncovers organic material (reviewed in Graf & Rosenberg 1997, Kristensen et al. 2012). Bioturbators can modify the position of particulate organic matter in the redox profile (e.g. Papaspyrou et al. 2004, Fanjul et al. 2015), speeding up or slowing down organic matter degradation. Whilst many burrow-dwelling species (e.g. polychaetes) subduct organic material deep (~10 cm) into the sediment (e.g. Levin et al. 1997, Shull & Yasuda 2001, Papaspyrou et al. 2004), other surface-dwelling bioturbators mix and expose organic matter at the surface (e.g. heart urchins; Lohrer et al. 2005, reviewed in Kristensen et al. 2012).

The combined role of organisms in changing sediment biogeochemistry and the vertical redistribution of organic matter in the sediment column is likely to have important feedbacks in areas of macrophyte detrital deposition (i.e. washed up detritus from seagrass, macroalgae, mangroves). In the laboratory, the feeding and irrigation behaviours of the polychaete *Nereis diversicolor* have been attributed to increased processing/degradation of algae detritus, and detrital N and C regeneration in marine sediments (e.g. Hansen & Kristensen 1998, Kristensen & Mikkelsen 2003, Papaspyrou et al. 2004). However, other macrofauna (e.g. lugworms, *Arenicola marina*) can actually slow down detrital recycling by subducting it to anoxic depths (Rossi et al. 2013). Thus, the bioavailability and cycling of marine macrophyte detritus, as well as how an ecosystem responds to detrital enrichment, depends largely on the functional behavioural traits of the dominant bioturbators.

Some herbivorous intertidal crab species construct semi-permanent burrows that efficiently trap detrital organic matter through passive deposition in burrow openings. Accordingly, intertidal crab burrow beds have been considered 'macrodetritus retention areas', as they effectively retain and recycle detritus within the system (e.g. Iribarne et al. 1997, 2000, Botto et al. 2006, Gutiérrez et al. 2006). Although these crabs may reduce the export of particulate organic material from the system, the ways in which this translates to ecosystem functions (e.g. benthic metabolism, primary production, and nutrient regeneration) requires further investigation.

In New Zealand, the common intertidal mud crab *Austrohelice crassa* (formerly *Helice crassa*; Family: Grapsidae), has displayed functional plasticity across sediment types, associated with differences in burrow permanency and rates of sediment reworking (Morrisey et al. 1999, Needham et al. 2010, 2011). In sandy permeable sediments, *A. crassa* mix and bulldoze sediments as burrows collapse and are reformed regularly, whereas in muddy cohesive sediments burrows persist for long periods and they fulfil the role of a burrow builder. As a result, rates of sediment reworking by *A. crassa* in sand are an order of magnitude greater than those in mud (Needham et al. 2010). These differences in burrow permanency and sediment reworking rates translate into differences in ecosystem function (Needham et al. 2011). In this study, we explored the consequences of this functional plasticity on detrital processing.

A manipulative field experiment was designed to establish how *A. crassa* and detritus (from the intertidal seagrass *Zostera muelleri*) interact to influence solute fluxes across the sediment–water interface (proxies for ecosystem function). We hypothesised that detrital degradation/processing would be enhanced in the presence of crabs, and that this interac-

tion would feed back to ecosystem function. Considering the functional plasticity displayed by *A. crassa* across sediment types (Needham et al. 2011), as well as the expected organic matter decay differences in sand versus mud (Hansen & Kristensen 1998, Rasheed et al. 2003), we also hypothesised that bioturbator–detritus interactions (and their effects on benthic ecosystem function) would differ between cohesive muddy sediments and permeable sandy sediments. We anticipated that the bulldozer/mixing behaviour of *A. crassa* in permeable sediments would play a role in accelerating detrital decay through increased sediment turnover and oxygenation, while their burrow-builder function in cohesive sediments may result in the burial of organic matter deeper within the anoxic sediments (effectively slowing down decay). This experiment was undertaken to increase our understanding of how changes in the amount of both benthic infauna and marine macrophytes (supply of detritus) will impact on coastal ecosystem function.

MATERIALS AND METHODS

Study site and experimental set-up

A field experiment to assess the role of bioturbator–detritus interactions on soft-sediment ecosystem function was established at 2 upper intertidal sites, described in Needham et al. (2011), in the Tairua Estuary, North Island, New Zealand. The sediment at the sand site (S) (37° 00′ 11.64″ S, 175° 50′ 46.05″ E) consisted of mainly fine permeable sands (median grain size 196 µm; 5% silt/clay content), while at the muddy-sand site (MS) (36° 59′ 53.36″ S, 175° 51′ 40.77″ E) the sediments were cohesive owing to a greater mud (i.e. silt/clay particles <63 µm) content (median grain size 243 µm; 14% silt/clay content). *Austrohelice crassa* are common in the intertidal areas throughout the Tairua Estuary (with adult densities up to 86 ind. m^{-2}; Needham et al. 2011), and the dominant macrophyte detrital source comes from the extensive intertidal *Zostera muelleri* beds within the estuary (~31 ha, 10% of the intertidal area; Felsing & Giles 2011).

To manipulate the presence and absence of both *A. crassa* and *Z. muelleri* detritus, 16 crab cages (0.4 × 0.6 × 0.6 m, h × l × w; 4 × 6 mm mesh) were partially buried (0.2 m) at each site. To remove large macrofauna (>2 mm; see Needham et al. 2011 for details) and homogenise the experimental units, the sediment in each cage was sieved (2 mm mesh) prior to treatment allocation. The experiment was conducted in summer, coinciding with peak seagrass production (Turner 2007), and high crab activity (Beer 1959, Nye 1974). Cages were arranged on the intertidal flat in 4 groups, with at least 2 m between each cage, and 5 m between groups (in a 20 × 20 m area). The slightly larger separation between groups of cages provided walking corridors through the study site to minimise disturbance during benthic chamber measurements. To ensure interspersion of treatments, one cage from each group was randomly assigned 1 of 4 experimental treatments: +Crabs+Detritus (+C+D), +Crabs–Detritus (+C–D), –Crabs+Detritus (–C+D), or –Crabs–Detritus (–C–D).

After deployment, the cages were left for ~21 d to re-establish natural sedimentary chemical gradients, after which 35 adult *A. crassa* (>8 mm carapace width) were introduced into +C cages (initial adult density of 97 ind. m^{-2}). *A. crassa* were translocated from the surrounding area on the same day. In order to account for crab losses during the experiment, the target initial density of *A. crassa* was chosen to be slightly greater than peak densities of adult crabs in the study area, and is equivalent to the highest crab density used by Needham et al. (2011). Crabs were left to re-establish for 4 d (~25 d after original cage deployment), before 130 g of dried *Z. muelleri* detritus (360 g m^{-2} dry weight; DW) was added to +D cages. The amount of detritus added was similar to that used in previous detrital addition experiments (e.g. Bishop et al. 2010, Taylor et al. 2010), and is realistic of detrital patch quantities observed in Tairua Estuary (R. V. Gladstone-Gallagher pers. obs.). Locally collected, fresh Z. *muelleri* blades were first dried to constant weight at 60°C to standardise detrital decay state and quantity. To mimic the natural deposition and desiccation of macrophyte detritus observed on intertidal flats, dried whole pieces of detritus were added to the cages by gently pressing into the sediment surface.

Field measurements

Ten to 12 d after the *Z. muelleri* detrital addition (~35 d after cages were established) benthic chambers (0.25 m^2) were deployed in the centre of each cage to measure fluxes of dissolved oxygen (DO) and ammonium (NH_4^+) across the sediment–water interface (as in Lohrer et al. 2004, Needham et al. 2011). This time frame was chosen to encompass the rapid initial breakdown of the litter (half-life of *Z. muelleri* is 28 d, but the fastest decay occurs within 0 to 4 d; see Gladstone-Gallagher et al. 2016). Metal chamber

bases (0.5 × 0.5 m) were pressed into the sediment within the cages at low tide, and transparent Perspex dome lids were fitted to seal a known volume (30 l) of water above the sediment surface on the incoming tide. Samples (50 ml) were drawn through 1.5 m of 3.2 mm diameter nylon tubing attached through the wall of the chamber. Samples were taken initially and then every 45 min for 4 h. To avoid stratification of the boundary layer, chamber water was recirculated using Sea-bird Electronics pulsed, non-directional pumps (SBE5M-1, 25 ml s^{-1} flow rate). DO was immediately measured in each water sample using a handheld DO probe (PreSens Fibox 3 PSt3), before being filtered (GF/C; 1.2 µm), and stored frozen in the dark for later inorganic nutrient analysis. HOBO loggers (5 min measurement interval) were placed inside 4 of the chambers during incubations to measure experimental light and water temperature just above the sediment–water interface. In order to obtain flux measurements from the same sediment patches in the presence and absence of sunlight, incubations were made during consecutive midday and midnight high tides. At low tide, between the day and night incubations, chamber lids were lifted off to re-equilibrate the system to ambient conditions, while the chamber bases were left in place. The meshed caging remained in place when the plots were unattended to prevent experimental crabs from escaping. On the next incoming tide (in the dark), chamber lids were re-fitted in order to initiate the dark incubations. Light DO fluxes were used to estimate net primary production by microphytobenthos (MPB), whereas dark incubations provided a measure of sediment community oxygen consumption (i.e. systemic metabolism in the absence of photosynthesis). During each incubation, three 1.5 l bottles were filled with ambient seawater and anchored just above the sediment surface, to correct measured fluxes for water column processes.

Once the incubations were completed, sediment properties were determined from 3 amalgamated cores (2.5 cm diam. × 2 cm depth) collected randomly from each incubation chamber. These samples were stored frozen and in the dark until laboratory analysis of sediment chlorophyll *a* (chl *a*), phaeopigment (phaeo), organic content (OC) and grain size (GS). Sediment cores were also collected from 4 uncaged positions at each site (*A. crassa* present) for comparison with the sediment properties within the cages. In addition, one core (13 cm diam., 15 cm depth) for the analysis of the macrofaunal community (i.e. fauna that could migrate through the 4 × 6 mm cage mesh) was taken from the centre of each cage, sieved on a 500 µm mesh, and the contents preserved in 70% isopropyl alcohol (IPA) awaiting species identification. Finally, sediment within the chambers was excavated to the bottom of the cage and sieved on a 2 mm mesh to recover all remaining crabs (preserved in 70% IPA) and seagrass detritus (frozen). The remaining sediment within the cage was also processed in this way to ensure that all of the crabs and seagrass detritus in the cages at the end of the experiment were accounted for.

Laboratory analyses

Filtered water samples from the chamber incubations were analysed for dissolved inorganic NH_4^+ on a LACHAT Quickchem 8500 series 2 Flow Injection Analyser. Other forms of inorganic nitrogen and phosphorus were not measured, because NH_4^+ has been found to be the dominant form of dissolved inorganic nitrogen released from sediments in New Zealand estuaries (>88%; e.g. Thrush et al. 2006, Sandwell et al. 2009, Jones et al. 2011, Pratt et al. 2014a,b, Gladstone-Gallagher et al. 2016), and temperate coastal primary production is thought to be generally regulated by nitrogen availability (Herbert 1999). Sediment OC was measured by drying sediment to constant weight (60°C), and then determining weight loss after furnace combustion (550°C for 4 h). Sediment chl *a* and phaeo content was determined by extracting pigments in 90% buffered acetone, and then measuring pigment content fluorometrically, before and after acidification (Turner 10-AU fluorometer; Arar & Collins 1997). Sediment GS was determined, after digestion in 10% hydrogen peroxide, on a Malvern Mastersizer 2000 (lasersizer particle size range: 0.05 to 2000 µm). Macrofauna were stained with Rose Bengal, sorted, and identified to the lowest practicable taxonomic level (usually species). The carapace width of all crabs collected from within the benthic chamber and the remaining cage area were measured using digital callipers, and the blotted wet weight determined. All seagrass detritus recovered from the cage was washed in freshwater, dried to constant weight (at 60°C), and weighed.

Data analysis

Solute fluxes were calculated using the slope of the linear regression of solute concentrations as a function of incubation time, sediment area, and chamber volume. Chamber flux calculations were also cor-

rected for water column processes measured in the bottles (usually <10% of the sediment flux). DO fluxes were used to infer net primary production (NPP; light DO flux), and community metabolism (sediment oxygen consumption, SOC; dark DO flux), as well as gross primary production (GPP; calculated from the difference between light and dark fluxes, i.e. NPP − SOC). In order to account for variability in MPB biomass, we normalised the GPP obtained in each cage by the respective sediment chl *a* content to provide an estimate of photosynthetic efficiency ($GPP_{chl\ a}$; i.e. gross production per unit of chl *a*). In this study, light and dark NH_4^+ fluxes were used as a proxy for the amount of inorganic nitrogen regenerated/taken up by the benthos.

Permutational analyses of variances (PERMANOVA) were used to compare solute fluxes, sediment properties, final crab density and biomass, detritus weights, macrofauna total abundance and species richness (Euclidean distance matrices on univariate data), as well as macrofauna community (Bray-Curtis similarity matrix on multivariate community data, excluding adult *A. crassa*) between treatment factors of crabs (fixed, 2 levels: +C and −C) and detritus (fixed, 2 levels: +D and −D), at each site separately. Since the experiment was conducted over a relatively small study area (20 × 20 m), and the experimental units were homogenised at the beginning of the experiment (sediments sieved), we did not anticipate a significant blocking effect on response variables. Initial analyses (with block as a random factor, and treatment as a fixed factor) confirmed that block was insignificant ($p > 0.05$ in all cases). Block was therefore excluded from subsequent PERMANOVA analyses in order to test for crab × detritus interactions. We chose to perform statistical tests for each site separately, because significant site × treatment interactions were found in preliminary analyses, and the variability in daytime light conditions made inter-site comparisons problematic (see 'Results'). We examined site-dependent treatment effects by interpreting how the treatment effects and their interactions differed between the sites. For significant factor interactions, post hoc PERMANOVA pair-wise tests were performed. We adopted an α level of 0.05, however in some instances we obtained p-values between 0.05 and 0.06. When present in combination with relatively large effect sizes (>50% difference in means), we reported these 'marginally significant' results also. SIMPER analysis (Bray-Curtis similarity) on the macrofaunal community data determined which taxa contributed to treatment differences. PERMDISP analysis confirmed homogeneity of multivariate dispersion among treatments ($p > 0.08$ at both sites). Raw, untransformed data were used in all PERMANOVA analyses, and all data analyses were done using the PRIMER 7 statistical software package, with the PERMANOVA+ addition (Anderson et al. 2008, Clarke & Gorley 2006).

RESULTS

Sediment properties and macrofauna

Treatment effects on sediment properties were only found at Site S, where the presence of crabs significantly reduced both the phaeo and mud content of the sediment (Table 1; $p = 0.009$ and 0.03, respectively; PERMANOVA results for sediment properties are given in Table A1 in the Appendix). No detrital-induced sediment anoxia was observed at either site (i.e. the surface brown oxic layer was present in both +D and −D treatments; Fig. 1). Sediment scouring around the cage edges did not occur, suggesting that cage–hydrodynamic interactions did not substantially alter the sedimentary environment within the cages. However, phaeo (at MS) and chl *a* (at S) ap-

Table 1. Mean sediment properties (1 SE in brackets, n = 4) for sites S (sand), and MS (muddy-sand), as a function of the presence and absence of *Austrohelice crassa* crabs (+C, −C) and detritus (+D, −D). Sediment properties for ambient uncaged sediments are also given for comparison with caged treatments. OC: sediment organic content; chl *a* = sediment chlorophyll *a* pigment content; phaeo: sediment phaeophytin pigment content; mud: particles <63 µm; GS: sediment grain size

Site	Treatment		Sediment properties				
	Crabs	Detritus	OC (%)	Chl *a* (µg g^{-1})	Phaeo (µg g^{-1})	Mud content (%)	Median GS (µm)
S	+C	+D	4.4 (0.2)	15.4 (1.6)	2.9 (1.2)	4.5 (0.4)	194 (4)
		−D	4.5 (0.5)	15.5 (2.7)	4.7 (0.4)	4.9 (0.9)	205 (11)
	−C	+D	4.4 (0.3)	15.8 (2.9)	5.9 (0.1)	6.2 (0.8)	191 (12)
		−D	5.1 (0.2)	21.2 (1.8)	5.8 (1.1)	6.3 (0.6)	189 (8)
	Ambient		5.1 (0.6)	28.2 (6.8)	3.9 (1.5)	4.6 (0.4)	196 (4)
MS	+C	+D	4.4 (0.4)	13.4 (1.3)	3.9 (1.6)	12.2 (2.8)	244 (33)
		−D	4.3 (0.2)	12.8 (1.3)	5.0 (0.4)	12.2 (3.5)	271 (17)
	−C	+D	4.8 (0.1)	14.1 (1.7)	4.8 (0.8)	15.6 (2.2)	225 (7)
		−D	4.2 (0.1)	11.6 (2.8)	2.7 (1.5)	11.4 (0.9)	270 (20)
	Ambient		4.6 (0.2)	14.4 (2.6)	8.4 (1.0)	13.6 (1.5)	243 (12)

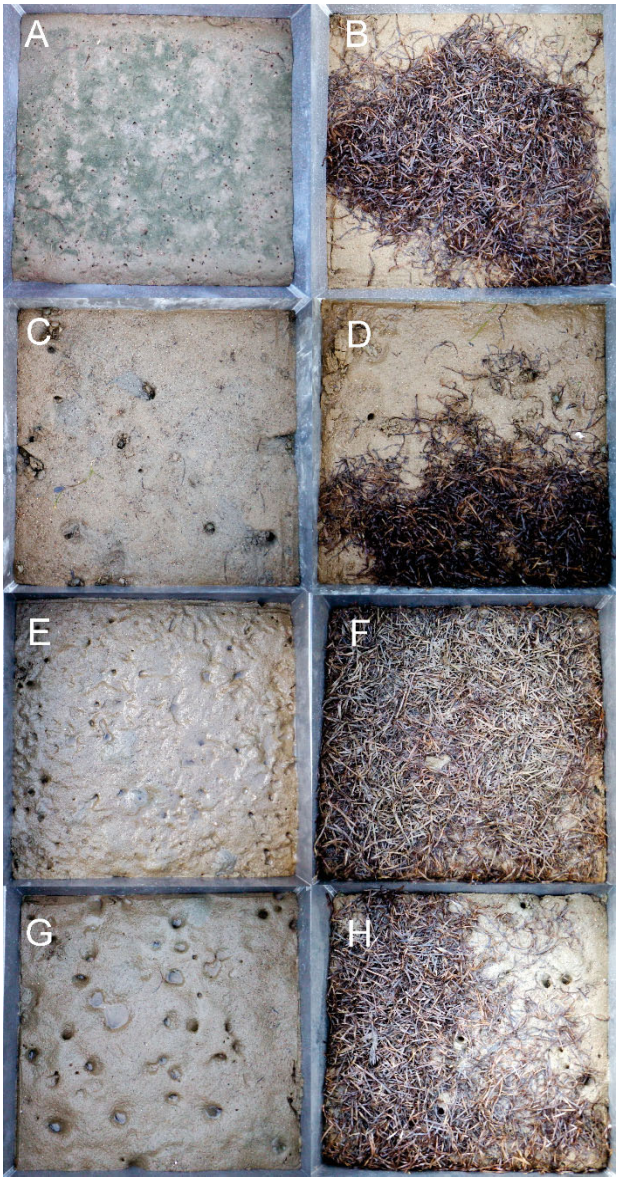

Fig. 1. Example photographs of the sediment surface in each treatment (presence or absence of *Austrohelice crassa* crabs, +C, −C; and detritus, +D, −D) at S (sand site): (A) −C−D, (B) −C+D, (C) +C−D, (D) +C+D; and at MS (muddy-sand site): (E) −C−D, (F) −C+D, (G) +C−D, (H) +C+D; photographs show the sediment enclosed within the 0.25 m^2 benthic incubation chamber

peared to be reduced (by 40 to 68% and 25 to 45%, respectively) in caged treatments compared to the surrounding ambient sediment (Table 1).

Visually, there was less detritus remaining on the sediment surface at S compared to MS, and there was also on average ~25% less seagrass detritus biomass recovered from the cages at S (Table 2, Fig. 1B,D vs. 1F,H). The presence of crabs also appeared to reduce the amount of detritus recovered from the +D cages by ~20% (Table 2), although this was not significant (crab effect p = 0.06 and 0.18 at S and MS, respectively; PERMANOVA results are given in Table A2 in the Appendix). Not all of the *Austrohelice crassa* introduced to +C cages at the beginning of the experiment were recovered at the end (Table 2), likely due to a combination of mortality and escapes (the proportion of each not known). Moreover, some crabs managed to enter −C cages. Nevertheless, at both sites, +C treatments had on average 2 to 4 times more adult *A. crassa* abundance and 5 times greater total biomass (which includes juveniles) than −C cages, and these differences were significant ($p < 0.005$; Tables 2 & A2).

There were significant treatment effects on macrofauna. The total abundance of macrofauna at MS was affected by the presence of detritus, with 6 times more individuals in −D cages than in +D cages (p = 0.0003; Tables 2 & A2). The treatments had no effect

Table 2. Mean (1 SE in brackets, n = 4) *Austrohelice crassa* crab density and biomass, and detritus measured in the experimental cages (0.36 m^2), as well as total macrofauna abundance and taxa richness (0.013 m^{-2}), for Sites S (sand) and MS (muddy-sand), as a function of the presence and absence of crabs (+C, −C) and detritus (+D, −D). DW: dry weight; BWW: blotted wet weight; juvenile *A. crassa*: carapace width <8 mm; adult *A. crassa*: carapace width >8 mm

Site	Treatment Crabs	Detritus	Final adult *A. crassa* (ind. $cage^{-1}$)	Adult *A. crassa* inside chamber (%)	Final juvenile *A. crassa* (ind. $cage^{-1}$)	Final *A. crassa* biomass (g BWW $cage^{-1}$)	Macrofauna abundance (ind. $core^{-1}$)	Macrofauna taxa richness (taxa $core^{-1}$)	Final detritus (g DW $cage^{-1}$)
S	+C	+D	20 (3)	67 (4)	4 (2)	19.1 (4.3)	44 (11)	9.5 (0.7)	37.8 (3.3)
		−D	26 (1)	79 (4)	3 (1)	23.1 (2.2)	42 (8)	6.3 (1.0)	0
	−C	+D	6 (1)	33 (4)	13 (5)	4.5 (1.0)	44 (10)	9.3 (1.9)	47.5 (4.1)
		−D	8 (2)	25 (12)	13 (3)	4.9 (0.7)	57 (11)	10.0 (0.5)	0
MS	+C	+D	20 (2)	76 (8)	11 (4)	15.2 (1.9)	30 (10)	7.8 (2.2)	50.5 (7.6)
		−D	16 (4)	59 (13)	6 (4)	13.6 (2.9)	103 (18)	5.8 (0.9)	0.5 (0.6)
	−C	+D	7 (2)	40 (13)	12 (4)	2.8 (0.6)	23 (4)	8.5 (0.7)	63.7 (7.4)
		−D	9 (5)	43 (20)	14 (4)	6.9 (4.8)	140 (10)	8.3 (2.5)	0

on total abundance at S, but there was a significant crab–detritus treatment interaction for taxonomic richness (p = 0.02). That is, the number of taxa was significantly lower in +C–D treatments relative to –C–D treatments at S (Tables 2 & A2). The nMDS ordinations of the macrofaunal community data (i.e. the community as a whole, excluding adult *A. crassa*) also showed different responses between sites. At S, treatment effects were not clear, as shown by the overlap in the nMDS points among treatments (Fig. 2A). In contrast, at MS, the clear clustering of the communities in +D cages compared to –D cages, as well as the wider spread of sample data from +D treatments, suggested that detritus added variability to the macrofauna community (Fig. 2B). These trends were also reflected in the community PERMANOVA analyses; community structure at S was unaffected by both treatments (although detritus effect marginally significant, p = 0.059; Table A2), whereas at MS, significant treatment effects were driven by detritus only (p = 0.0004; Table A2). SIMPER analysis revealed that the community differences between treatments at MS were driven primarily by a decrease in the amphipod *Paracorophium excavatum* in +D cages (in comparisons between +D and –D cages, *P. excavatum* alone contributed to >80% of the dissimilarity).

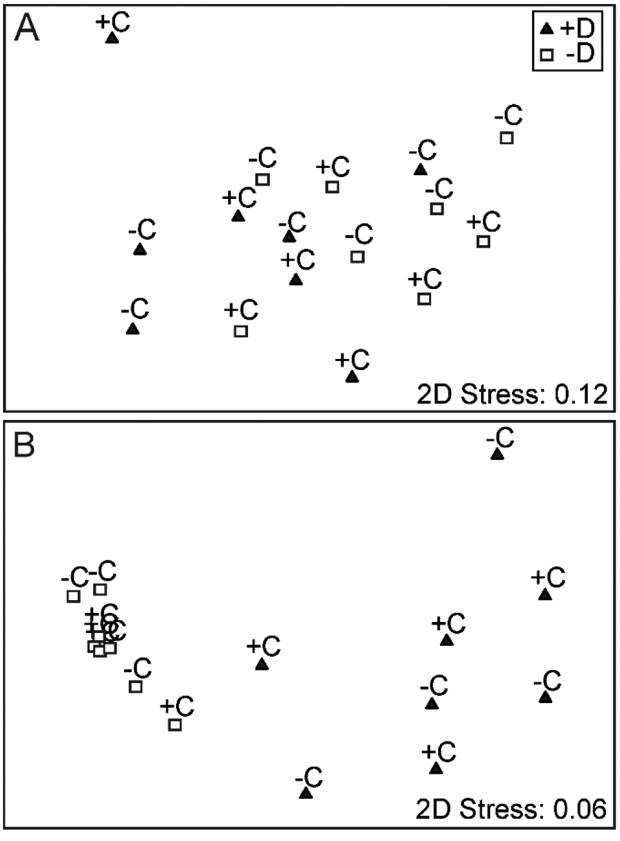

Fig. 2. Non-metric multi-dimensional scaling (nMDS) analysis (Bray-Curtis similarity) for (A) site S (sand), and (B) MS (muddy-sand), showing differences in the macrofaunal community composition (excluding adult *Austrohelice crassa*), as a function of the presence and absence of crabs (+C, –C) and detritus (+D: black triangles; –D: white squares). Each point on the ordination represents the community in each flux chamber

Benthic ecosystem function

Treatment effects on dark DO flux magnitude were site-dependent. At S, SOC rates were 12 to 21% higher in +C treatments compared to –C (p = 0.04), with no detrital treatment effects. Whereas at MS, 12 to 29% more SOC occurred in +D treatments compared to –D (p = 0.01), with no crab treatment effects (Fig. 3, Table 3). NH_4^+ fluxes were mostly positive, indicating an efflux of NH_4^+ out of the sediment; however, in a few cases (–C treatments), NH_4^+ fluxes were negative or close to zero. At S, dark NH_4^+ efflux was 75 to 82 µmol N m^{-2} h^{-1} in +C cages, while in –C cages fluxes were negative, indicating an uptake by the sediments rather than an efflux (p = 0.002), and the effect of crabs was significant regardless of the detrital treatment (i.e. no C × D interaction; Fig. 4A, Table 3). A similar result was observed in light chambers, where NH_4^+ efflux was 6 times greater in +C than in –C cages and independent of detrital treatment (Fig. 4B, Table 3). In contrast, dark NH_4^+ fluxes at MS were variable and affected by both crab and

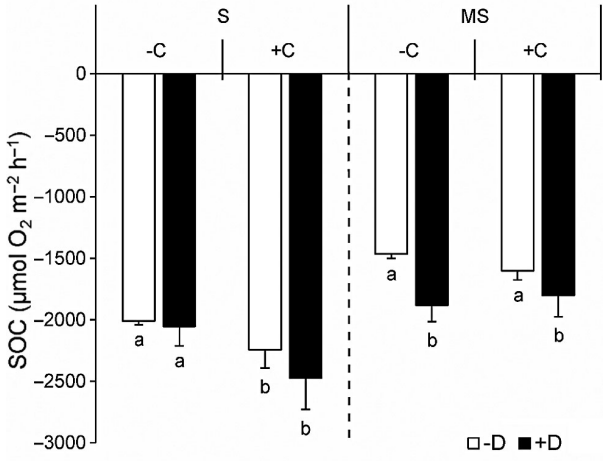

Fig. 3. Mean (+1 SE, n = 4) sediment oxygen consumption (SOC), as a function of site (S: sand; MS: muddy-sand), and presence or absence of *Austrohelice crassa* crabs (+C, –C) and detritus (+D: black bars; –D: white bars). PERMANOVA pair-wise test results for significant effects are depicted as letters, where bars sharing the same letter within a site are not significantly different (p > 0.05). Full PERMANOVA results are given in Table 3

Table 3. Results of PERMANOVA (Euclidean distance) comparing measures of ecosystem function between *Austrohelice crassa* crab (C; 2 levels: +C, −C) and detritus (D; 2 levels: +D, −D) treatments at each site (S: sand; MS: muddy-sand). Significant results are indicated in **bold** ($p < 0.05$), and pair-wise post hoc results are given for significant interactions. Main effects are only considered in the absence of an interaction. SOC: sediment oxygen consumption; NPP: net primary production; GPP: gross primary production; $GPP_{chl\ a}$: GPP normalised for chl *a* biomass; NH_4^+: ammonium flux; +C: crabs present; −C: crabs absent; +D: detritus present; −D: detritus absent

Site	Variable	Source	df	MS	Pseudo-*F*	p-value	Pair-wise tests
S	SOC	C × D	1	34000	0.405	0.5449	
		C	1	432620	5.149	**0.0439**	+C > −C
		D	1	73365	0.873	0.3700	
		Residual	12	84028			
	NH_4^+ (dark)	C × D	1	5	0.002	0.9700	
		C	1	40620	12.632	**0.0025**	+C > −C
		D	1	140	0.044	0.8392	
		Residual	12	3216			
	NH_4^+ (light)	C × D	1	474	2.542	0.1374	
		C	1	14052	75.436	**0.0001**	+C > −C
		D	1	237	1.272	0.2768	
		Residual	12	186			
	NPP	C × D	1	4198800	9.979	**0.0091**	+D: +C = −C; −D: −C > +C +C: −D > +D[a] ; −C: −D > +D
		C	1	10154000	24.131	0.0005	
		D	1	21664000	51.486	0.0001	
		Residual	12	420770			
	GPP	C × D	1	4899100	11.881	**0.0057**	+D: +C = −C; −D: −C > +C +C: −D = +D ; −C: −D > +D
		C	1	6496600	15.756	0.0025	
		D	1	19392000	47.031	0.0001	
		Residual	12	412340			
	$GPP_{chl\ a}$	C × D	1	56	0.014	0.8945	
		C	1	3319	0.818	0.3877	
		D	1	28308	6.980	**0.0254**	−D > +D
		Residual	12	4055			
MS	SOC	C × D	1	47824	1.180	0.2931	
		C	1	3301	0.081	0.7838	
		D	1	383340	9.457	**0.0123**	+D > −D
		Residual	12	40535			
	NH_4^+ (dark)	C × D	1	9364	5.002	**0.0295**	+D: +C = −C; −D: +C > −C[a] +C: +D = −D; −C: +D = −D
		C	1	3406	1.819	0.2091	
		D	1	259	0.138	0.7640	
		Residual	12	1872			
	NH_4^+ (light)	C × D	1	385	0.451	0.5100	
		C	1	725	0.848	0.3742	
		D	1	51	0.060	0.8149	
		Residual	12	854			
	NPP	C × D	1	1850	0.012	0.9049	
		C	1	219570	1.479	0.2439	
		D	1	106360	0.716	0.4056	
		Residual	12	148490			
	GPP	C × D	1	30861	0.208	0.6471	
		C	1	169020	1.139	0.3036	
		D	1	85864	0.578	0.4546	
		Residual	12	148440			
	$GPP_{chl\ a}$	C × D	1	7×10^{-2}	4.452×10^{-5}	0.9950	
		C	1	1988	1.300	0.2877	
		D	1	12	0.008	0.9409	
		Residual	12	1529			

[a]Indicates post hoc pair-wise test p = 0.057

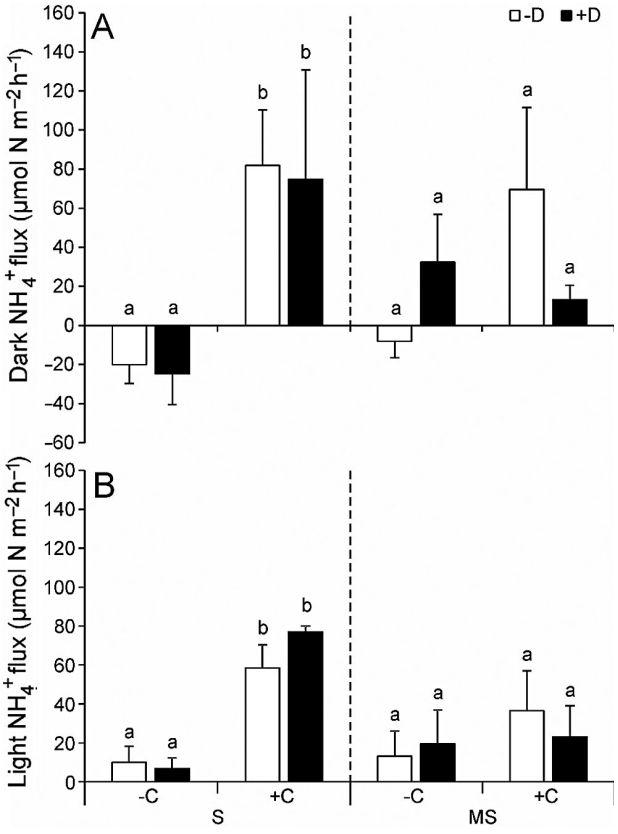

Fig. 4. Mean (+1 SE, n = 4) (A) dark and (B) light ammonium fluxes (NH_4^+), as a function of site (S: sand; MS: muddy-sand), and presence or absence of *Austrohelice crassa* crabs (+C, –C) and detritus (+D: black bars; –D: white bars). PERMANOVA pair-wise test results for significant effects are depicted as letters, where bars sharing the same letter within a site are not significantly different ($p > 0.05$). Full PERMANOVA results are given in Table 3

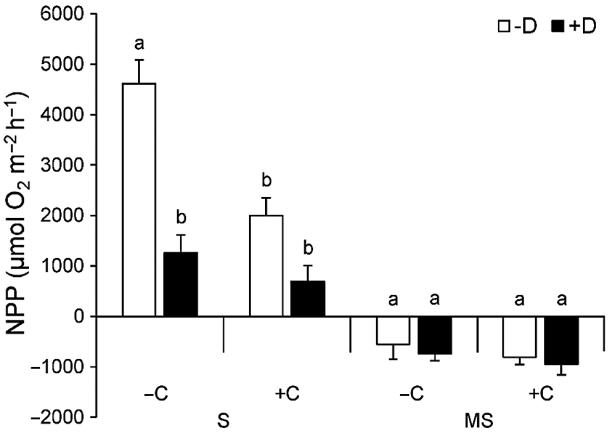

Fig. 5. Mean (+1 SE, n = 4) net primary production (NPP), as a function of site (S: sand; MS: muddy-sand), and presence or absence of *Austrohelice crassa* crabs (+C, –C) and detritus (+D: black bars; –D: white bars). PERMANOVA pair-wise test results for significant effects are depicted as letters, where bars sharing the same letter within a site are not significantly different ($p > 0.05$). Full PERMANOVA results are given in Table 3

detrital treatments (C × D interaction, $p = 0.03$). Whilst none of the pair-wise tests were significant, the comparison between +C–D and –C–D cages was marginally significant ($p = 0.057$), suggesting a crab effect on dark NH_4^+ flux, but only in the absence of detritus at MS (Fig. 4A, Table 3). Light NH_4^+ fluxes were unaffected by treatment at MS (Fig. 4B, Table 3).

Daytime light levels at the seabed during chamber incubations varied by an order of magnitude between sites (S = 24381 ± 11937 lux, and MS = 2081 ± 812 lux; mean ±1 SE, n = 4), and these differences appeared to influence photosynthetic rates. DO flux in light chambers (NPP) at S was positive, indicating that photosynthetic oxygen production was greater than total community oxygen demand during the incubation period (Fig. 5), whereas at MS, where light levels were naturally lower due to increased turbidity, NPP was negative. At S, both crabs and detritus decreased NPP, where the mean individual effects approximately equalled their combined effects (Fig. 5). There was a C × D interaction at Site S ($p = 0.009$), and pair-wise comparisons revealed that crabs decreased NPP, but only in the absence of detritus ($p = 0.03$). Detritus also suppressed NPP, both in the absence ($p = 0.03$) and presence of crabs (although only marginally significant, $p = 0.057$; Table 3). Similar treatment effects were found for GPP at S (Fig. 6A, Table 3). On the other hand, $GPP_{chl\,a}$ at S was decreased (by ~28 %, $p = 0.03$) in the presence of detritus, but there was no crab effect (Fig. 6B, Table 3). At MS, NPP, GPP, and $GPP_{chl\,a}$ were unaffected by treatment (Figs. 5 & 6, Table 3).

DISCUSSION

In this *in situ* experiment, we manipulated the presence/absence of *Austrohelice crassa* and the supply of detritus (from *Zostera muelleri*) to explore how interactions between bioturbating crabs and detrital deposition influence ecosystem function in soft-sediment habitats. Although the densities of crabs that were recovered from cages at the end of our experiments differed from the initial target densities of 0 and 35 ind. $cage^{-1}$ (in –C and +C cages, respectively), crab densities nevertheless differed significantly by treatment at both our study sites. By comparing ecosystem responses in these low and high crab density treatments, we were able to demon-

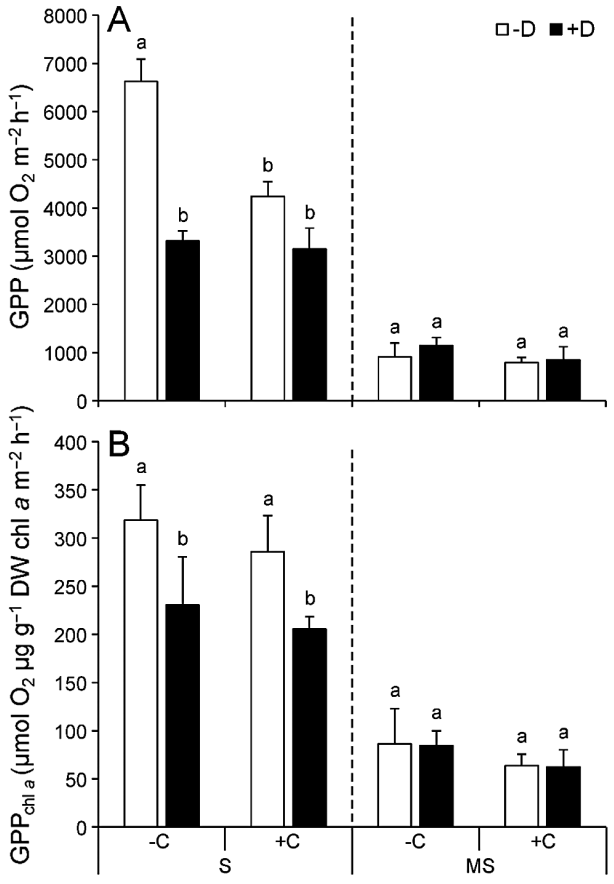

Fig. 6. Mean (+1 SE, n = 4) (A) gross primary production (GPP) and (B) gross primary production normalised for chlorophyll *a* biomass ($GPP_{chl\ a}$), as a function of site (S: sand; MS: muddy-sand), and presence or absence of *Austrohelice crassa* crabs (+C, −C) and detritus (+D: black bars; −D: white bars). PERMANOVA pair-wise test results for significant effects are depicted as letters, where bars sharing the same letter within a site are not significantly different ($p > 0.05$). Full PERMANOVA results are given in Table 3

strate effects of *A. crassa* on key ecosystem functions at both sites. At Site S, crabs dominated the effects on benthic metabolism (i.e. SOC) and NH_4^+ regeneration (light and dark fluxes), and no detrital effects were observed. Conversely, at MS, effects on SOC were dominated by detritus (with no crab effect). This lack of crab effect may be associated with the larger variability and smaller differences in final crab densities between the +C and −C treatments at our muddy-sand site. However, crabs did affect dark NH_4^+ flux at this site, but only in the absence of detritus. Our results highlight the context-dependent role of detrital subsidies in modifying ecosystem function of intertidal soft-sediments.

Treatment effects on benthic metabolism were site-specific, where SOC was stimulated in +C treatments in sandy permeable sediments, but in the muddy-sand SOC was enhanced in +D treatments. Crab density is understood to be positively correlated with sediment oxygen demand, associated with both the respiratory demands of these animals and the indirect effects of bioturbation on sediment biogeochemistry (Needham et al. 2011). Respiration rates for *A. crassa* in New Zealand estuaries indicate this species consumes ~6.8 µmol O_2 g^{-1} DW h^{-1} (Shumway & Jones 1981, Hawkins et al. 1982), which when scaled to the crab biomass in our cages would account for 24 to 52% of the difference in SOC between −C and +C treatments (at S). Accordingly, the crab treatment effect on SOC in the sandy sediments can only be partially explained by crab respiration. In general, the fauna-mediated oxygen consumption (i.e. indirect effects on sediment biogeochemistry and microbial respiration) has been previously found to exceed the respiratory demands of many bioturbators (reviewed in Glud 2008). Site differences in crab treatment effects on SOC may be confounded by the variability in the final densities of crabs remaining in the treatments between sites. However, the differences can also be plausibly explained by the higher activity and sediment reworking that is associated with the higher frequency of burrow rebuilding by *A. crassa* in sandier sediments (Needham et al. 2010). Associated with increased sediment mixing and activity, we also found that at high densities (i.e. +C), crabs reduced the sediment mud content when compared to low density −C treatments, but this only occurred in the sandy sediments, reaffirming *A. crassa*'s functional plasticity across sedimentary gradients.

Detrital breakdown is enhanced and facilitated by oxygen consuming bacteria (Sun et al. 1993, Hulthe et al. 1998, Kristensen 2000), and so we anticipated that detrital addition would stimulate SOC. However, detrital treatment effects on SOC were only found in the muddy-sand sediments. Detrital recovery in the sand was also ~25% less than in the muddy-sand (see Table 2), indicating either greater decay in the permeable sediments or hydrodynamically enhanced export through the mesh. Site differences in detrital effects on SOC may therefore be driven by differences in detrital loss between sites, with detrital effects on SOC being greatest in muddy-sand where detrital loss was lowest. Alternatively, the effects of detritus on soft-sediment ecosystem function may be more apparent in cohesive sediments that typically have a higher background organic content (Trask 1938, Mayer et al. 1985, Thrush et al. 2012, Pratt et al. 2014a). As such, increasing organic loading in already organically enriched sediments may cause stronger responses in ecosystem function associated

with organic matter 'priming' (i.e. inputs of new organic matter may stimulate the remineralisation of background organic matter; Hee et al. 2001, van Nugteren et al. 2009).

Site-specific treatment responses were also found in the community of fauna that were small enough to migrate through the cage mesh. As with SOC, detrital effects on the macrofaunal community were only significant in the muddy-sand. Treatment differences were driven, in part, by the increased variability in the community with the addition of detritus (i.e. the wide spread of +D sample data in Fig. 2B). Additionally, in the muddy-sand, detrital addition drove a large decrease in the abundance of suspension-feeding amphipods. Our results highlight that detrital enrichment can influence community structure by altering the relative abundances of species. Benthic solute fluxes are understood to be influenced by macrofaunal biodiversity and abundance (Lohrer et al. 2004, Hewitt et al. 2006, Kristensen et al. 2014, Norkko et al. 2015), and our detrital induced shifts in macrofaunal abundances in the muddy-sand may have contributed to the observed changes in function (i.e. direct decay effects vs. indirect effects via macrofaunal community changes). Furthermore, the role of detritus in structuring benthic macrofaunal communities has been found in other temperate intertidal settings (e.g. Kelaher & Levinton 2003, Bishop et al. 2010, O'Brien et al. 2010), and our results confirm that the ecological effects of detrital enrichment are likely to be context-specific, depending on the sediment type of the depositional environment.

In tropical climates, numerous studies have highlighted the functional role of crabs in enhancing leaf litter decay, through shredding and/or ingestion (Robertson 1986; reviewed in Lee 1998). We measured 20% less detritus remaining in +C cages compared to –C cages, and although not statistically significant, we suggest that this result highlights a potential role of crabs in detrital matter removal. While increased detrital burial caused by burrowing can slow down decay (Rossi et al. 2013), other examples show that macrofauna can increase the decay of marine leaf litter detritus, both through bioirrigation (which increases the oxygen in the sediments available for aerobic decay), and ingestion (which increases surface area for microbial colonisation of the organic matter) (e.g. reviewed in Harrison 1989, Lillebø et al. 1999, Kristensen & Mikkelsen 2003, Proffitt & Devlin 2005). Whether enhanced loss of detritus from +C cages was due to direct effects of the crabs, including consumption and increased fragmentation, or indirect effects resulting from enhanced remineralisation or physical export of detritus through sediment mixing and destabilisation remains unknown. However, since we found no evidence of synergistic effects of crabs and detritus on SOC or NH_4^+ fluxes, it is unlikely that crabs enhanced detrital remineralisation. Furthermore, since *A. crassa* derive much of their diet from grazing on MPB (Alfaro et al. 2006), detrital loss through consumption/ingestion was probably minimal. However, by physically enhancing detrital export from the benthic system, *A. crassa* may influence the removal of deposited organic material on intertidal flats, and this is likely greater in sand where *A. crassa* are more active at reworking the sediments (Needham et al. 2010).

As laboratory studies have previously found fauna to enhance organic matter remineralisation (e.g. Hansen & Kristensen 1998, Kristensen & Mikkelsen 2003, Papaspyrou et al. 2004), we expected to find synergistic effects of crabs on NH_4^+ regeneration in the presence of detritus. Instead, as with SOC, the NH_4^+ fluxes in sand were only affected by crabs (i.e. there were no detrital treatment effects or interactions), where *A. crassa* enhanced NH_4^+ effluxes (in both light and dark chambers) from the sediments at high densities. NH_4^+ fluxes out of the sediments are often high in sediments inhabited by large macrofauna (including crabs), which is attributed to both excretion and the release of NH_4^+ from the pore water during bioturbation (e.g. Fanjul et al. 2011, Jones et al. 2011, Needham et al. 2011, Norkko et al. 2013). Assuming a respired oxygen:excreted nitrogen ratio of 27.8 (found for *Hemigrapsus crenulatus*; Urbina et al. 2010) and using respiration rates for *A. crassa* (Shumway & Jones 1981, Hawkins et al. 1982) reveals that NH_4^+ excretion rates are likely to represent <26% of the NH_4^+ fluxes measured in this study. This confirms that crab effects are mostly associated with indirect bioturbation effects, which has also been suggested by Woodin et al. (2016) for deposit feeding bivalves *Macomona liliana* and heart urchins *Echinocardium cordatum*. Seagrass detritus, on the other hand, represents a low quality nitrogen resource (mean leaf N <2%; reviewed in Duarte 1990) in temperate estuaries, and therefore NH_4^+ remineralisation during decay may be minimal and/or too low to detect as a flux across the sediment–water interface.

Our ability to detect detrital treatment effects may also have been limited by only measuring NH_4^+ fluxes if detritus enhances nitrification/denitrification pathways that rapidly convert NH_4^+ into other forms of inorganic nitrogen. Water column nitrate concentrations are low in many New Zealand estuaries

(Jones et al. 2011, Pratt et al. 2014a), and therefore in oxic sediments (like those at our sandy site) nitrification and denitrification are coupled. This means that nitrification of NH_4^+ into NO_3^- (in the oxic sediments) is immediately denitrified into N_2 in the underlying anoxic layer (Rysgaard et al. 1994, Sloth et al. 1995, Seitzinger et al. 2006). Thus, remineralised detrital NH_4^+ may have been rapidly converted to NO_2^-, NO_3^-, or N_2, limiting our ability to detect detrital treatment effects on NH_4^+ regeneration at our sandy site. Having said this, in a previous field experiment conducted at a sandy site, seagrass, mangrove and kelp detritus did not increase NO_2^- or NO_3^- fluxes across the sediment–water interface (Gladstone-Gallagher et al. 2016).

At MS, results suggest that crabs enhanced dark NH_4^+ efflux, but only in the absence of detritus (Table 3). The lack of crab effect in the presence of detritus could be due to changes in crab behaviour that reduced the contribution of excretion and/or bioturbation to NH_4^+ efflux (e.g. a reduction in crab burrowing or foraging behaviours). Another possibility is that the addition of detritus influenced sediment biogeochemistry (note that SOC was also increased by detritus at MS) and nitrification/denitrification pathways, thereby affecting the form of nitrogen released from the sediment. Both benthic fauna and organic matter enrichment can independently and interactively increase rates of nitrification and denitrification (e.g. Caffrey et al. 1993, Sloth et al. 1995, Dunn et al. 2012). For example, faunal activities can increase rates of nitrification by burying organic detritus, creating anoxic microniches that are sites of increased denitrification (e.g. Dunn et al. 2012). Perhaps similar fauna–organic matter interactions stimulated coupled nitrification/denitrification in our study, rapidly removing the excess NH_4^+ from pore waters before it entered the water column. The interaction between crabs and detritus on benthic NH_4^+ regeneration demonstrates the potential role of detritus in modifying ecosystem processes on crab dominated mudflats, and the need for further investigation.

Two separate treatment processes affected benthic primary production in sandy sediments. Both crabs and detritus reduced NPP, and their combined effects approximately equalled their individual effects (C × D interaction; although not all pair-wise tests were significant). NPP is a measure of photosynthetic production minus oxygen consumed during respiration of the benthos, while $GPP_{chl\,a}$ gives the total production per unit of MPB biomass. Thus, the significant detrital treatment effects on $GPP_{chl\,a}$ suggest that detritus reduces the photosynthetic efficiency of MPB productivity regardless of changes to biomass. The detrital inhibition of both NPP and $GPP_{chl\,a}$ is therefore likely to be associated with the shading effect that detritus has on the sediment surface. Because the crab treatment had no effect on $GPP_{chl\,a}$, their effects on NPP and GPP is likely explained by the fact that grazing reduces MPB biomass at high crab densities. Observations of the sediment surface in –C–D cages at the sand site showed a MPB biofilm that was not obvious in other treatments, supporting the interpretation that *A. crassa* reduces benthic primary production via grazing (compare Fig. 1A and 1C). Treatment effects on NPP, GPP, and $GPP_{chl\,a}$ were not found at our muddy-sand site, and site comparisons of these ecosystem functions were not possible because of the variable and low light conditions during daytime incubations.

We added whole seagrass detritus, realistic of what enters the system, but in many previous studies, detritus has been added in a ground form or slightly buried to simulate the incorporation of partially decayed and fragmented organic matter into the sediments (e.g. Kelaher & Levinton 2003, Bishop et al. 2010, Gladstone-Gallagher et al. 2016). The form in which detritus enters a system could influence the ecosystem response. Ecosystem responses to detritus enrichment are temporally variable, and fragmented detritus can suppress primary production in the short term (4 d), but enhance it over longer temporal scales (2 to 3 wk; Gladstone-Gallagher et al. 2016). Leaf surface area is known to affect decomposition rate (Harrison & Mann 1975), and here, primary production was suppressed 10 d after the detrital addition, perhaps suggesting that positive effects on ecosystem function may be delayed with whole detritus. One of the limitations of our experimental design is that, due to destructive sampling (necessary to determine final crab and other macrofauna densities), we only gained a snapshot of the functionality of the system at one time point. This has particular relevance when studying detrital enrichment, as the importance of the detritus may be more apparent at different stages of its decay, and further investigations are required to try to tease apart the interacting processes of decay stage, and the natural temporal variability in soft-sediment ecosystem function (Morrisey et al. 1992, Thrush et al. 1994, Hewitt et al. 2007).

At a global scale, seagrass habitats are in decline (Inglis 2003, Moore & Short 2006) and loss of biodiversity in coastal systems is predicted to rise (Snelgrove et al. 2014). Changes in the abundance of functionally important species, such as seagrass and key macrofaunal species like *A. crassa* are likely to im-

pact on the functioning of coastal ecosystems and the goods and services they provide. *In situ* manipulations highlight the complexities of functional interactions in coastal habitats, and help to tease apart the relationships in a more realistic manner than laboratory studies alone. Here, we demonstrated that *in situ* crab–detritus interactions behaved differently than indicated from individual effects in controlled laboratory studies on functionally similar species (e.g. Hansen & Kristensen 1998). Our study suggests that detrital subsidies can have negative effects on ecosystem function in muddier habitats dominated by burrowing crabs by reducing the efflux of NH_4^+, a critical source of nitrogen sustaining primary production in New Zealand estuaries. However, in muddy sediments, detrital enrichment may also be important for regulating ecosystem function by stimulating benthic metabolism and altering macrofaunal community structure. Compared to the muddy-sand site, the effects of detritus were less at the sandy site, which appears to be more functionally robust as detrital subsidies did not induce large shifts to ecosystem function (except through shading effects on primary production). Our results emphasise that sediment context is paramount when understanding the effects of changes in biodiversity on ecosystem function.

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Appendix

Table A1. Results of PERMANOVA (Euclidean distance) tests comparing sediment properties between *Austrohelice crassa* crab (C; 2 levels: +C, –C) and detritus (D; 2 levels: +D, –D) treatments, at each site (S: sand; MS: muddy-sand). Significant results are indicated in **bold** ($p < 0.05$), and pair-wise post hoc results are given for significant interactions. Main effects are only considered in the absence of an interaction. OC: sediment organic content; chl *a*: sediment chlorophyll *a* pigment content; phaeo: sediment phaeophytin pigment content; mud: particles <63 µm; GS: sediment grain size; +C: crabs present; –C: crabs absent; +D: detritus present; –D: detritus absent

Site	Variable	Source	df	MS	Pseudo-*F*	p-value	Pair-wise tests
S	OC	C × D	1	0.33	1.01	0.3299	
		C	1	0.45	1.38	0.2579	
		D	1	0.54	1.64	0.2222	
		Residual	12	0.33			
	Chl *a*	C × D	1	27.67	1.70	0.1997	
		C	1	37.06	2.27	0.1532	
		D	1	30.93	1.90	0.1855	
		Residual	12	16.31			
	Phaeo	C × D	1	3.24	1.48	0.2489	
		C	1	16.58	7.57	**0.0094**	–C > +C
		D	1	2.91	1.33	0.2887	
		Residual	12	2.19			
	Mud content	C × D	1	0.08	0.06	0.8125	
		C	1	9.48	6.69	**0.0251**	–C > +C
		D	1	0.17	0.12	0.7334	
		Residual	12	1.42			
	Median GS	C × D	1	169.61	0.68	0.4409	
		C	1	368.28	1.49	0.2498	
		D	1	84.07	0.34	0.5782	
		Residual	12	247.97			
MS	OC	C × D	1	0.23	1.04	0.3313	
		C	1	0.06	0.28	0.6019	
		D	1	0.33	1.52	0.2459	
		Residual	12	0.22			
	Chl *a*	C × D	1	3.76	0.36	0.5671	
		C	1	0.31	0.03	0.8631	
		D	1	9.79	0.93	0.3460	
		Residual	12	10.56			
	Phaeo	C × D	1	10.18	2.50	0.1398	
		C	1	2.23	0.55	0.4658	
		D	1	0.95	0.23	0.6401	
		Residual	12	4.07			
	Mud content	C × D	1	17.61	0.90	0.3433	
		C	1	6.27	0.32	0.5754	
		D	1	17.15	0.88	0.3651	
		Residual	12	19.53			
	Median GS	C × D	1	298.60	0.22	0.6310	
		C	1	370.18	0.27	0.6170	
		D	1	5266.10	3.84	0.0700	
		Residual	12	1369.80			

Table A2. Results of PERMANOVA tests comparing *Austrohelice crassa* crab density/biomass, total macrofaunal abundance, species richness, and final detritus (Euclidean distance), as well as the macrofaunal community structure (Bray-Curtis similarity) between crab (C; 2 levels: +C, −C) and detritus (D; 2 levels: +D, −D) treatments, at the sand site (S) and muddy-sand site (MS). Significant results are indicated in **bold** ($p < 0.05$), and pair-wise post hoc results are given for significant interactions. Main effects are only considered in the absence of an interaction. DW: dry weight; +C: crabs present; −C: crabs absent; +D: detritus present; −D: detritus absent

Site	Variable	Source	df	MS	Pseudo-*F*	p-value	Pair-wise tests
S	Final adult *A. crassa* density	C × D	1	14	1.64	0.2058	
		C	1	1073	125.26	**0.0001**	+C > −C
		D	1	60	7.01	**0.0248**	−D > +D
		Residual	12	9			
	Final juvenile *A. crassa* density	C × D	1	2	0.05	0.8425	
		C	1	371	11.35	**0.0024**	−C > +C
		D	1	3	0.09	0.7664	
		Residual	12	33			
	Final *A. crassa* biomass	C × D	1	12	0.64	0.4236	
		C	1	1078	57.46	**0.0002**	+C > −C
		D	1	19	1.04	0.3238	
		Residual	12	19			
	Total macrofauna abundance	C × D	1	156	0.62	0.4465	
		C	1	132	0.53	0.4727	
		D	1	156	0.62	0.4454	
		Residual	12	250			
	Macrofauna taxa richness	C × D	1	16	7.25	**0.0196**	−D: −C > +C; +D: −C = +C −C: −D = +D; +C: −D > +D[a]
		C	1	12	5.55	0.0393	
		D	1	9	4.08	0.0687	
		Residual	12	2			
	Macrofauna community structure	C × D	1	594	0.58	0.3062	
		C	1	1110	1.08	0.3490	
		D	1	2115	2.05	0.0586	
		Residual	12	1031			
	Final detritus DW	C × D	1	94	4.48	0.0721	
		C	1	94	4.48	0.0606	
		D	1	7278	344.97	**0.0001**	+D > −D
		Residual	12	21			
MS	Final adult *A. crassa* density	C × D	1	39	1.19	0.2893	
		C	1	452	13.73	**0.0051**	+C > −C
		D	1	5	0.15	0.6896	
		Residual	12	33			
	Final juvenile *A. crassa* density	C × D	1	49	0.89	0.3593	
		C	1	81	1.47	0.2563	
		D	1	12	0.22	0.647	
		Residual	12	55			
	Final *A. crassa* biomass	C × D	1	33	1.27	0.2685	
		C	1	365	13.85	**0.0045**	+C > −C
		D	1	6	0.23	0.6270	
		Residual	12	26			
	Total macrofauna abundance	C × D	1	1620	1.90	0.1936	
		C	1	885	1.04	0.3214	
		D	1	38123	44.72	**0.0003**	−D > +D
		Residual	12	853			
	Macrofauna taxa richness	C × D	1	2	0.24	0.6231	
		C	1	9	0.98	0.3475	
		D	1	4	0.43	0.5128	
		Residual	12	9			
	Macrofauna community structure	C × D	1	1238	1.01	0.3403	
		C	1	736	0.60	0.6173	
		D	1	18733	15.26	**0.0004**	+D ≠ −D
		Residual	12	1227			
	Final detritus DW	C × D	1	187	2.21	0.1441	
		C	1	161	1.90	0.1828	
		D	1	12940	152.89	**0.0001**	+D > −D
		Residual	12	85			

[a]Indicates post hoc pair-wise test is significant at $p = 0.0561$

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