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An examination of the spatial and temporal generality of the influence of ecosystem engineers on the composition of associated assemblages

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Abstract The present study evaluated the generality of ecosystem engineering processes by examining the influence of sympatric burrowing shrimps (Callianassidae) and intertidal seagrasses (Zosteraceae) on benthic assemblage composition in two temperate regions, south-eastern New Zealand and north-western U.S.A. In each region, intertidal macrofauna assemblage composition was determined at sites of different burrowing shrimp/seagrass density and where both species co-occured, in three different size estuaries/tidal inlets, on two occasions. Results from both regions showed that the presence of shrimps and seagrasses consistently influenced the composition of the associated infaunal assemblages at all sites, in both summer and winter. Macrofauna assemblages at shrimp sites were significantly different to those at seagrass-only and mixed sites, whereas the composition of the latter sites was similar. The differences observed between sites were best explained by sediment variables. In New Zealand, % fines and seagrass debris showed the highest correlation to differences in assemblage composition, and in the U.S.A. % fines, % carbon and sediment turnover (by shrimp) appeared to be the most important environmental parameters measured. Four to six taxa exhibited the greatest discriminating significance (including corophiid amphipods, spionid polychaetes and oligochaetes) for dissimilarities in assemblage composition observed at the different sites, with generally lower abundances at shrimp than at seagrass sites. The present study highlights the functional importance of seagrasses and bioturbating shrimps as ecosystem engineers in soft-sediment environments, and reveals the generality of their influence on associated macroinvertebrate assemblages. The findings also allow for further development of a heuristic model for ecosystem engineering by shrimp and seagrass which indicate that numerical models that aim to explore the relationship between ecosystem engineer populations and habitat modification should be expanded to capture the interaction of co-occurring engineers and be both spatially and temporally explicit.

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Introduction

Ecologists concerned with the organisation of natural communities have long recognised the importance of species that have a disproportionate influence on assemblage composition. Some organisms, such as so-called 'keystone' or 'foundation' species, profoundly impact associated organisms in an assemblage through predation and competition; and ecological experiments and theory have predominantly focused on considering how these biotic interactions structure terrestrial and aquatic assemblages (Paine 1966; Dayton 1972; Schoener 1983). However, relatively recent ecological studies have highlighted the importance of abiotic interactions between organisms and their environment, which can be equally dramatic to those of keystone species, but are not included in the current ecological framework (Bertness 1985; Jones et al. 1994; Bruno et al. 2003). Jones et al. (1994) tried to address this shortfall by proposing the concept of organisms as "physical ecosystem engineers". This notion encompasses interactions between organisms and their environment that are not directly trophic or competitive, and which result in the modification, maintenance and/or creation of habitats. That is, rather than providing resources directly, ecosystem engineers physically change their environment and impact the supply of resources for other species, thereby affecting species abundance and diversity, population, community and ecosystem stability (Jones et al. 1994). Jones et al. (1994) distinguished between two kinds of engineers: 'Autogenic engineers' impact the habitat in which they live through their own physical structures and are an integral part of the engineered ecosystem. 'Allogenic engineers', on the other hand, modulate resources from one physical state to another through their behaviour and activity.

Following the initial proposal of the concept, a number of studies illustrated its application to terrestrial and aquatic habitats by providing examples of plants and animals as autogenic or allogenic ecosystem engineers; e.g. *Sphagnum* moss (van Breemen 1995) and detritivorous tropical fish (Flecker 1996). In the marine environment, bioturbators have been presented as classic examples of ecosystem engineers (Levinton 1995), as they affect physical and biogeochemical properties of the sediment, such as near-surface sediment stability, sediment grain size, organic content and nutrient loading; environmental parameters which affect the habitat suitability for other species (de Wilde 1991). However, application of the formal assessment criteria for recognising and scaling the influence of ecosystem engineers (Jones et al. 1994) has been lacking for marine bioturbators until very recently.

Callianassid shrimps (Thalassinidea), also referred to as ghost, burrowing or mud shrimps, are a ubiquitous group of decapod crustaceans that have long been recognised as significant infaunal bioturbators of intertidal and shallow subtidal soft sediments (Suchanek 1983; Swift 1993; Cadée 2001). Application of the formal ecosystem engineer assessment criteria to one such ghost shrimp, *Callianassa filholi*, identified this species as an important allogenic ecosystem engineer, which influenced macrofauna assemblage composition over a small spatial scale through its large *per capita* bioturbation activity (Berkenbusch and Rowden 2003). Having established the engineering significance of this species (endemic to New Zealand) in one intertidal habitat raises the question as to whether ghost shrimp species are generally important in structuring assemblage composition across similar habitats at different spatial scales. The study on the impact of *Callianassa filholi* bioturbation on associated community assemblages also indicated that the engineering influence of the ghost shrimp was moderated by the presence of a small intertidal seagrass *Zostera capricorni* (previously *Zostera novozelandica*, see Les et al. 2002) which buffered the effect of the shrimp during summer, when seagrass biomass was high. *Zostera capricorni* can be considered an autogenic ecosystem engineer, as seagrasses, for example, provide living space for others through their own physical structure (Berkenbusch et al. 2000, and see conceptual model in Berkenbusch and Rowden 2003). The temporally manifested moderation of the influence of one type of engineering species on that of another raises the question as to whether such an interaction generally occurs between ghost

shrimps and seagrasses, which frequently co-occur in the same habitats.

Thus, the present study aimed to assess the generality of ecosystem engineering processes for sympatric allogenic engineering shrimps (Callianassidae) and autogenic engineering seagrasses (Zosteraceae). Specifically, we addressed the following questions: (1) Do ghost shrimps and seagrasses consistently influence associated benthic assemblages over different spatial scales and time? and (2) What are the potential mechanisms by which these ecosystem engineers exert their influence on associated macrofauna assemblages? Addressing such questions allows for the exploration of what Jones et al. (1997) term 'multiple engineers and coupled and uncoupled interactions' and 'coupled engineering and trophic cascades', the development of the local heuristic ecosystem engineering model earlier proposed for shrimp and seagrass (Berkenbusch and Rowden 2003), and the potential to develop or parameterize the models of ecosystem engineering proposed by Gurney and Lawton (1996).

Materials and methods

Study design and sampling

The study was conducted in two temperate regions 1,000s of km apart, south-eastern New Zealand and north-western United States of America (U.S.A.) (Fig. 1a and b). Within each region, three estuaries/tidal inlet locations were selected that were 10s of km apart and which contained both ghost shrimp and seagrass within the same intertidal area. Estuaries/inlets were selected to have different areas, but with similar tidal regimes across regions. In New Zealand, study locations were Otago Harbour (46 km^2), Blueskin Bay (6.9 km^2) and Papanui Inlet (3.5 km^2). In the U.S.A., the study locations were Tillamook Bay (33.5 km^2), Yaquina Estuary (15.8 km^2) and Netarts Bay (9.4 km^2). All estuaries/tidal inlets were characterised by semi-diurnal tides with a similar tidal range (1.4–2.2 m in New Zealand, 1.3–2.9 m in the U.S.A.). Ghost shrimps included in the study were *Callianassa filholi* in New Zealand, and *Neotrypaea californiensis* in the U.S.A. Both callianassid species are burrowing deposit-feeders, of similar size (12–16 mm adult carapace length) and commonly occur in intertidal soft-sedimentary habitats in their respective regions (MacGinitie 1934; Devine 1966). Corresponding seagrass species were *Zostera capricorni* and *Zostera japonica* in New Zealand and the U.S.A., respectively. Both intertidal seagrasses are small (approx. 15 cm average leaf length), perennial species, that form dense monospecific beds of several km^2 and exhibit seasonal fluctuations in biomass, i.e. above-ground material, with a substantial increase during spring and summer (Inglis 2003). Whilst *Zostera capricorni* is native to New Zealand, *Zostera japonica* has reportedly been introduced to the west coast of the U.S.A. with
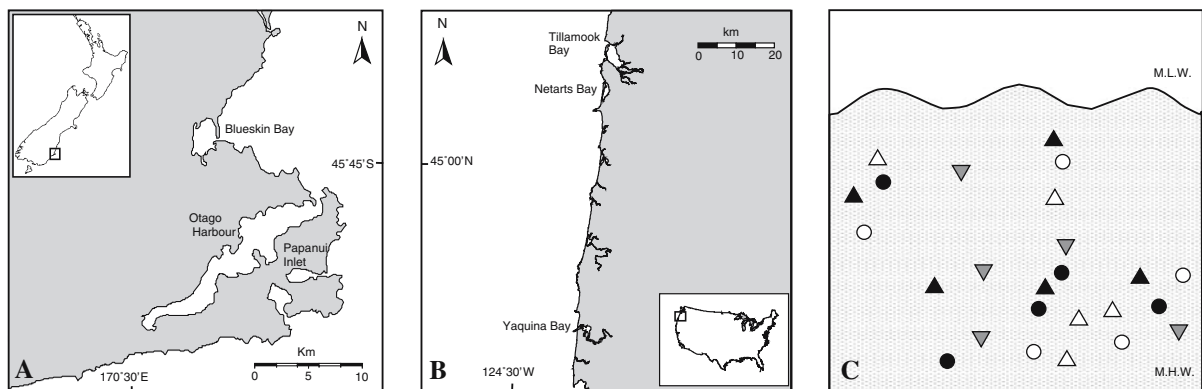
Fig. 1 Location of study sites in south-eastern New Zealand (**A**), north-western U.S.A. (**B**), and schematic layout of treatment sites (**C**) of seagrass (circles), shrimp (triangles), and mixed (inverted triangles) treatment sites within each estuary/inlet (low-density = open, high-density = filled, mixed = grey)

oyster imports in the 1800s (Harrison and Bigley, 1982).

Within each location, "treatment" sites (ca. 2×2 m) were chosen to reflect naturally occurring high and low densities of either shrimp or seagrass, and where both organisms co-occured ('mixed'). Different shrimp and seagrass densities were included as treatments in order to ascertain the relative level at which the influence of either engineering organisms is reflected in macrofauna assemblage composition. Initial selection of density groupings was made in summer at sites where shrimp and seagrass were homogenously distributed. In each location, 'low' and 'high' density groupings were based on at least a two-fold difference in abundance, measured by the number of mounds m^{-2} and number of shoots m^{-2}, respectively (Table 1). Mixed sites contained a range of shrimp and seagrass density, generally representing low to intermediate levels of both. Each treatment was replicated five times, and replicates

were haphazardly interspersed across the tidal range of shrimp/seagrass-habitat area (Fig. 1c). Latitude and longitude of each replicate treatment site was determined using GPS, and replicates were marked with coloured pegs to ease subsequent relocation for sampling of macofauna assemblages and measurement of selected environmental parameters.

Environmental parameters chosen for measurement were those that were likely to reflect a direct or indirect influence of the two ecosystem engineers studied. Samples were collected during summer (January 2002, New Zealand; June/July 2002, U.S.A.) and winter (August 2002, New Zealand; January/February 2003, U.S.A.) to account for seasonal differences in shrimp bioturbation activity and seagrass phenology.

On each sampling occasion, the number of shrimp mounds within a 0.25 m^2 quadrat was recorded in shrimp treatments. This non-destructive proxy measure of shrimp density was validated

Table 1 Mean values (±SE) of number of seagrass shoots (78.5 cm^{-2}) and number of shrimp sediment expulsion mounds (0.25 m^{-2}) from treatment sites at each location and region, summer and winter (hZ/lZ = high-/low-density seagrass, hS/lS = high-/low-density shrimp, mix = mixed treatments)

	# Shoots	# Mounds	# Shoots	# Mounds	# Shoots	# Mounds
New Zealand	Otago Harbour		Blueskin Bay		Papanui Inlet	
Summer						
hS	0	14.80±1.77	0	10.40±1.33	0	20.80±2.52
lS	0	3.00±1.05	0	3.20±0.73	0	6.20±1.85
hZ	52.20±7.75	0	60.40±6.17	0	84.80±9.62	0
lZ	31.40±9.37	0	20.40±5.84	0	27.20±6.51	0
Mix	37.00±10.45	8.40±1.60	37.20±6.06	3.00±0.32	31.00±5.35	6.40±1.50
Winter						
hS	0	15.00±2.47	0	6.20±1.85	0	11.20±1.59
lS	0	3.20±0.20	0	2.60±0.51	0	2.80±0.66
hZ	37.40±12.87	0	40.80±9.68	0	47.80±8.35	0
lZ	22.40±4.62	0	35.00±5.61	0	22.60±1.89	0
Mix	28.20±4.49	5.00±1.30	37.80±5.14	1.20±0.37	24.40±4.21	1.80±0.37
USA	Tillamook Bay		Yaquina Bay		Netarts Bay	
Summer						
hS	0	8.80±1.16	0	21.80±2.42	0	28.80±3.65
lS	0	1.40±0.24	0	10.60±1.89	0	4.00±1.14
hZ	16.60±1.63	0	37.60±6.17	0	27.20±2.01	0
lZ	7.20±1.85	0	14.80±5.09	0	10.00±2.59	0
Mix	9.20±2.22	3.60±0.51	15.60±4.48	15.00±4.28	15.80±2.40	4.80±1.62
Winter						
hS	0	3.80±0.37	0	3.40±0.75	0	15.80±4.36
lS	0	1.20±0.37	0	100±0.32	0	2.20±0.58
hZ	8.20±0.49	0.20±0.20	28.80±4.95	0.00±0.00	5.00±2.14	0.60±0.60
lZ	9.40±2.82	0	17.60±3.08	0	2.60±1.44	0.80±0.37
Mix	5.20±1.11	1.60±0.40	11.20±3.62	1.60±0.24	4.40±1.69	3.00±0.84

simultaneously in adjacent (i.e. non-sampled) areas where mound numbers were related to shrimp density. Shrimp were sampled in three representative areas of each low, high and mixed shrimp mound density by using a mega-core (29 cm Ø, 50 cm depth). Sediment from each core was sieved on 3 mm mesh and shrimp retained on the mesh were anaesthetised (7.5% magnesium chloride in freshwater) for 5 h prior to fixation in 10% formalin/seawater. Shrimp were subsequently counted, sexed, and measured (carapace length; tip of the rostrum to the posterior margin of the carapace).

Prior to collection of macrofauna samples at treatment sites, seagrass above-ground biomass was sampled in the same area by placing a plastic ring (10 cm Ø) on the sediment surface and cutting off all shoot material within it. Shoots and leaves were rinsed in freshwater (to remove associated fauna and any adhering sediment) and counted. Plant material was then dried (48 h at 60°C) and weighed (±0.0001 g). Fauna associated with the above-ground component of the seagrass were not retained for analysis. Samples of sediment macrofauna were collected using a core (10 cm Ø, 10 cm depth), the contents of which were sieved on 500μm mesh, and preserved in 70% isopropyl alcohol with 0.2% rose bengal. Retained invertebrates were identified to the lowest practical taxonomic level (generally species) and counted using microscopy. Only sediment macrofauna were sampled in order to allow for an examination of the influence of ecosystem engineers on a single component of the associated benthos. Seagrass below-ground material (rhizomes and roots) was separated from faunal samples, rinsed in freshwater, dried (48 h at 60°C) and weighed (±0.0001 g). Unattached, dead and senescent seagrass material (debris) was also sorted from macrofauna samples, rinsed in freshwater, dried (48 h at 60°C) and weighed (±0.0001 g).

Sediment characteristics

Cores were taken for sediment grain size, carbon, nitrogen (same core 3 cm Ø, 10 cm depth) and chlorophyll *a* (2.5 cm, 2 cm depth) analysis. Sediment samples were kept dark and chilled, before being frozen prior to laboratory analysis. Samples for sediment grain size were digested in 6% hydrogen peroxide for 24 h to remove organic matter. Subsequently, percent volumes for sediment fractions were determined by wet-sieving (particle size >850 μm) and by using a laser diffraction particle size analyser (particle size < 850 μm). Sediment samples for organic carbon and nitrogen analysis were freeze-dried and treated with 0.1 N HCl to remove inorganic carbon (Hedges and Stern 1984). Weight percent carbon and total nitrogen was determined using a CHN analyser. Chlorophyll *a* was extracted by boiling a homogenised and freeze-dried sediment sample in 90% ethanol. The extract was analysed using a spectrophotometer, and included an acidification step to separate degradation products from cholorophyll *a* (Sartory 1982).

Ghost shrimp bioturbation activity was assessed on each sampling occasion by trapping sediment expelled from shrimp burrows over a 24 h period. Sediment traps consisted of plastic containers (11 cm Ø) with a 1 cm hole in the bottom for expelled sediment to enter through, and bolting mesh on top (110 micron) to prevent loss of sediment from the trap. Three burrows were haphazardly selected at each shrimp and mixed treatment site, and sediment traps were placed carefully over the burrow expulsion hole (revealed after removing the mounds), and secured with wire stakes. An equal number of control traps were deployed at the same time within each treatment site (including seagrass only treatments). After 24 h, sediment traps were collected and sediment from the traps was washed in freshwater to remove salt, dried (48 h at 70°C) and weighed (±0.0001 g).

Data analysis

The relationship between number of mounds and number of shrimp was determined by linear least squares regression (Zar 1974) for each region and season. The validity of the high- and low-density treatments were tested for each location and season using non-parametric Kruskal–Wallis tests applied to shoot and mound density data.

A non-parametric multivariate approach was used to analyse data from the present study because it provides a particularly useful (e.g.

sensitive) means to determine and explore any observed differences in assemblage composition (Warwick and Clarke 1991; Clarke 1993). Data were analysed using PRIMER (Plymouth Routines in Multivariate Ecological Research) (Clarke and Gorley 2001), a suite of computer programs for multivariate analysis (see Clarke and Warwick 2001). Macrofauna abundance data were square-root-transformed prior to the construction of a ranked similarity matrix based on the Bray–Curtis index (Bray and Curtis 1957). A square-root transformation was applied to raw data to balance the contribution of common and rare species in the similarity measure between samples (Clifford and Stephenson 1975). Differences in macrofauna assemblage compositions were visually assessed using non-metric multidimensional scaling (MDS) ordinations (Field et al. 1982), and formally tested by applying two-way crossed analysis of similarities (ANOSIM) (Warwick et al. 1990) for each region and season, with location and treatment as factors.

Following formal testing, the similarity procedure SIMPER (Clarke 1993) and correlation-based BVSTEP (Clarke and Warwick 2001) were used to provide explanations for the patterns observed and thereby elucidate the possible mechanisms by which associated assemblage composition might be influenced. Taxa contributing to (% average contribution to overall dissimilarity), and that best discriminate between (when the ratio of a taxon's average contribution to dissimilarity/standard deviation of the contribution to the dissimilarity is >1.3, see Clarke and Warwick 2001, p. 7-3), dissimilarities observed between treatments were determined using SIMPER. The relationship between multivariate assemblage composition and the measured normalised environmental parameters was investigated in a stepwise approach using BVSTEP. Environmental parameters included in the latter analysis were number of shoots, number of leaves, seagrass above- and below-ground biomass, seagrass debris, shrimp mound density, expelled sediment turnover, % organic C, % total N, sediment chlorophyll a, % sand (sediment particles >63 μm), % 'fines' (silt and clay particles, <63 μm). Variables were checked for co-correlation using Spearman's Rank Correla-

tion (cut-off ρ = 0.95); number of leaves, % N, % sand were subsequently omitted from the analysis. Variables were also visually checked for conformation to multivariate normality using 'draftsman plots' (Clarke and Ainsworth 1993); seagrass debris and expelled sediment turnover were subsequently log-transformed prior to analysis.

Results

In New Zealand, 54–64 taxa were identified at the locations (tidal inlets/estuaries) sampled, with 41 of the taxa shared by all locations in the region. The number of taxa sampled at locations in the U.S.A. was lower, ranging from 37–54 taxa, of which 27 taxa were common to all locations in the region.

In each region, there was a significant linear relationship between number of mounds and number of shrimp sampled using the mega-core each season (F: 12.28–54.64, P: 0.0001–0.0017, r^2 values: 0.33–0.69). Kruskal–Wallis tests established that the number of seagrass shoots and the number of shrimp mounds at each site were significantly different (d.f. = 4, χ^2: 14.20–23.30, P < 0.01) for all study locations in both seasons. That is, counts of shrimp mounds are an acceptable proxy for shrimp density and the allocated sites were valid treatments in which naturally occurring differences between shrimp and seagrass density were evident at all estuaries/inlets in summer and winter.

MDS ordinations of macrofauna data showed a consistent pattern across regions, with a clear separation between shrimp and seagrass treatment sites in each location during summer and winter (Fig. 2A–D). Macrofauna assemblages at mixed sites were generally similar to those at seagrass sites, and there was apparently little dissimilarity in assemblage composition between low- and high-density treatment groupings, in particular for seagrass sites. Two-way crossed ANOSIM permutation tests confirmed the visual interpretation of the MDS plots, indicating that dissimilarities between locations and treatments were significant for each region and season (Table 2). For both regions in both seasons,
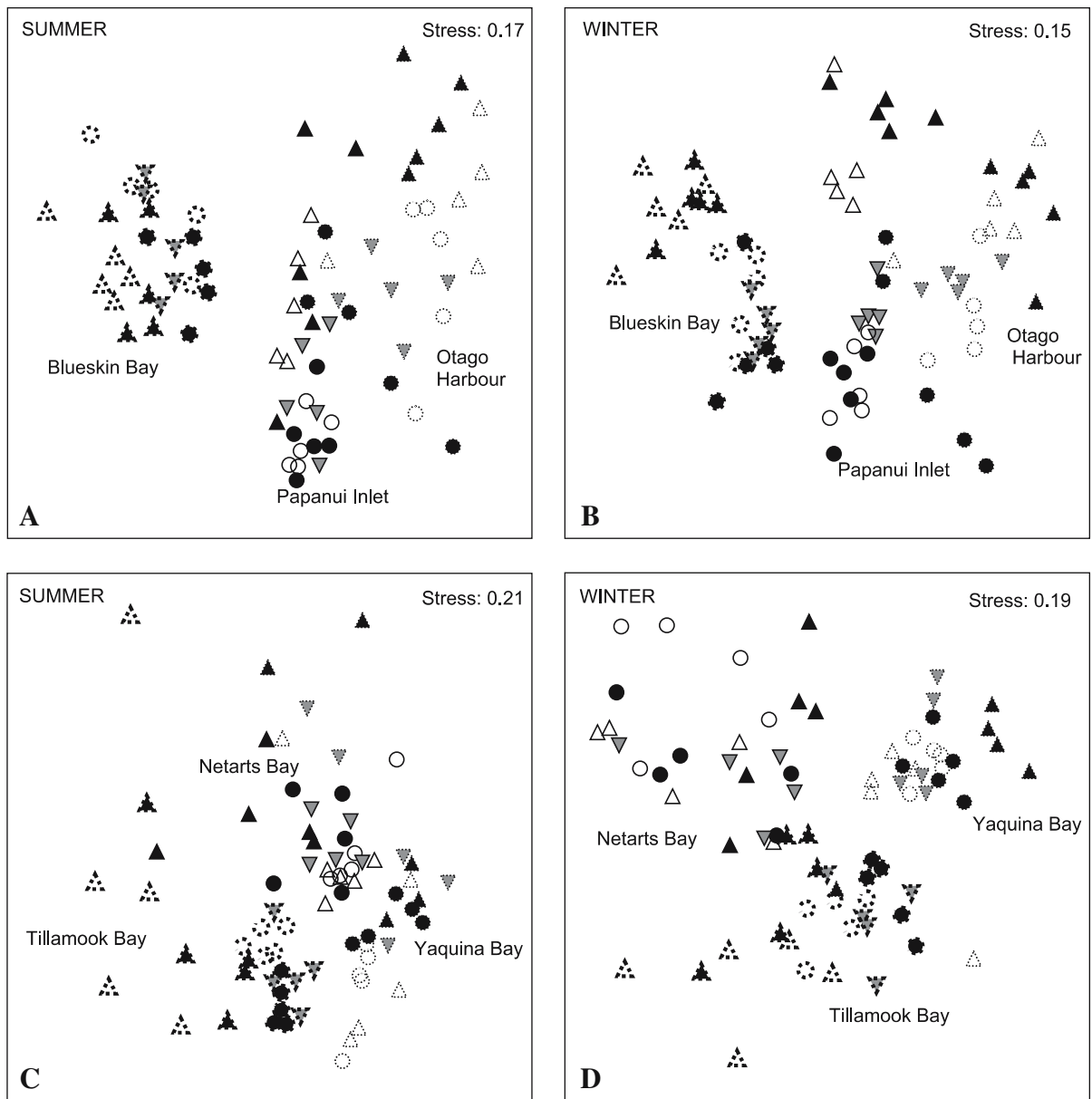
Fig. 2 MDS ordinations of infaunal macrofauna abundance data (square-root-transformed) from treatment sites at locations in New Zealand (**A** and **B**) and the USA (**C** and **D**) in winter and summer (Treatments: seagrass = circles, shrimp = triangles, mixed = inverted triangles; low-density = open, high-density = filled, mixed = grey).

differences in macrofauna assemblage composition were greater between locations (Global R: 0.710–0.915) than between treatments (Global R: 0.226–0.471). Pair-wise tests revealed that differences between treatments were generally consistent across locations and regions, and were greatest between shrimp and seagrass treatments (R: 0.403–0.873, P = 0.001 all cases) than between

high- and low-density sites of seagrass/shrimp treatments (R: 0.025–0.593, P = 0.355–0.001). Differences in assemblage composition for the latter were generally greater in the summer than in the winter (exception: high/low density seagrass in New Zealand region). Assemblage composition at mixed treatment sites was always significantly dissimilar ($P < 0.05$ all cases) from

Table 2 Summary of results from 2-way ANOSIM for differences between locations and treatments including global and pairwise significant levels between treatments in each region for both seasons (hZ/lZ = high-/low-density seagrass, hS/lS = high-/low-density shrimp, mix = mixed treatments)

Summer

		hS R	hS P	lS R	lS P	hZ R	hZ P	lZ R	lZ P
New Zealand									
Location R = 0.915, P = 0.001	IS	**0.025**	0.355						
Treatment R = 0.396, P = 0.001	hZ	**0.748**	0.001	**0.684**	0.001				
	lZ	**0.691**	0.001	**0.495**	0.001	**0.275**	0.003		
	Mix	**0.588**	0.001	**0.373**	0.001	**0.097**	0.127	**0.088**	0.153
USA									
Location R = 0.789, P = 0.001	IS	**0.281**	0.003						
Treatment R = 0.347, P = 0.001	hZ	**0.403**	0.001	**0.533**	0.001				
	lZ	**0.541**	0.001	**0.205**	0.001	**0.593**	0.001		
	Mix	**0.263**	0.006	**0.337**	0.002	**0.199**	0.009	**0.427**	0.001

Winter

		hS R	hS P	lS R	lS P	hZ R	hZ P	lZ R	lZ P
Location R = 0.906, P = 0.001	IS	**0.107**	0.086						
Treatment R = 0.471, P = 0.001	hZ	**0.873**	0.001	**0.716**	0.001				
	lZ	**0.703**	0.001	**0.549**	0.001	**0.177**	0.016		
	Mix	**0.800**	0.001	**0.595**	0.001	**0.329**	0.001	**0.112**	0.064
Location R = 0.710, P = 0.001	IS	**0.140**	0.052						
Treatment R = 0.226, P = 0.001	hZ	**0.491**	0.001	**0.325**	0.003				
	lZ	**0.409**	0.001	**0.179**	0.012	**0.183**	0.023		
	Mix	**0.299**	0.001	**0.203**	0.012	**0.061**	0.202	**0.008**	0.425

that at shrimp treatment sites (*R*: 0.299–0.800), but generally not dissimilar from seagrass treatment sites (exceptions: high-density/winter/New Zealand, low-density/summer/U.S.A). Global and pair-wise differences between treatments were generally greater for the New Zealand than the U.S.A. region.

Application of similarity percentages (SIM-PER) analyses to macrofauna abundance data for significantly different treatment groups (data were pooled for locations and combined where treatments were not significantly different from one another) revealed the extent of the average dissimilarity between treatments/treatment groupings in each region for summer and winter, and identified those taxa that contributed most to the dissimilarity observed and/or discriminated between the groups examined (Tables 3 and 4). In New Zealand, average dissimilarity between shrimp (low and high-density treatments) and 'seagrass' (low and/or high-density and mixed treatments) assemblage composition in summer and winter was approximately the same (66/67%) (Table 3). Taxa that contributed the most (6–9%) to the dissimilarities observed between these treatment groupings were also similar in both seasons. That is, the polychaete Paraonidae sp. 1 and the bivalve mollusc *Perrierina turneri* were consistently more abundant in the shrimp than in the seagrass treatment grouping, whilst abundance of oligochaetes was the converse. Taxa that best discriminated between the treatment groupings were the amphipod crustacean *Protophoxus australis* and the spionid polychaete *Aquilaspio aucklandica* in summer, whilst the syllid polychaete *Exogone* sp. 1 and oligochaetes discriminated between the treatment groupings in winter. All of the four discriminating taxa showed lower abundances in the shrimp than in the seagrass treatment groupings.

In the U.S.A., average dissimilarity between shrimp (low and/or high-density treatments) and 'seagrass' (low or high-density and mixed treatments) assemblage composition in summer and winter was relatively similar (51–58%) (Table 4). Average dissimilarity between high- and low-density shrimp treatments was slightly higher (62%), whilst dissimilarity between high- and low-density seagrass, and low-density and mixed treatments,

Table 3 Results from SIMPER analysis including mean abundance (α) and dissimilarity (DS) of macrofauna taxa averaged between significantly different treatments for summer and winter in New Zealand, the ratio ($\bar{\delta}i/\mathrm{SD}\delta i$) the percentage ($\delta i\%$) and cumulative percentage contribution ($\sum\delta i\%$) to the average Bray–Curtis dissimilarity between treatment groupings (cut-off to taxa list applied at 50% cumulative contribution to dissimilarity; those taxa with a ratio >1.3 are highlighted in bold)

New Zealand				
Summer				
α_S	α_Z	$\bar{\delta}i/\mathrm{SD}\delta i$	$\delta i\%$	$\sum\delta i\%$
(α_S = lS & hS; α_Z = hZ & Mix) DS = 66.42%				
Paraonidae sp. 1 — 28.0	19.43	0.96	8.05	8.05
Perrierina turneri — 26.17	6.83	0.8	6.46	14.51
Oligochaeta — 14.73	36.3	1.25	6.31	20.82
Exogone sp. 1 — 15.27	12.43	1.28	5.15	25.96
Protophoxus australis — **5.93**	**15.97**	**1.38**	**5.12**	**31.09**
Nucula hartvigiana — 11.93	13.27	1.28	5.06	36.15
Paracalliope novizealandiae — 3.6	8.83	1.21	3.78	39.94
Ostracoda sp. 1 — 1.07	6.63	1.03	3.33	43.27
Aquilaspio aucklandica — **4.4**	**5.6**	**1.33**	**3.13**	**46.4**
Paracorophium excavatum — 10.77	6.47	0.55	3.12	49.52
(α_S = lS & hS; α_Z = lZ & Mix) DS = 67.11%				
Paraonidae sp. 1 — 28.0	16.6	0.99	7.95	7.95
Perrierina turneri — 26.17	152.3	0.89	7.14	15.09
Oligochaeta — 14.73	44.17	1.23	7.11	22.2
Exogone sp. 1 — 15.27	19.0	1.26	5.73	27.93
Paracorophium excavatum — 10.77	21.27	0.67	4.93	32.86
Protophoxus australis — **5.93**	**14.17**	**1.36**	**4.91**	**37.76**
Nucula hartvigiana — 11.93	12.6	1.25	4.89	42.65
Paracalliope novizealandiae — 3.6	10.4	1.08	4.04	46.69
Puyseguria turneri — 11.5	3.2	0.68	3.01	49.7
Winter				
(α_S = lS & hS; α_Z = hZ & lZ & Mix) DS = 66.12%				
Perrierina turneri — 51.93	27.29	0.94	9.02	9.02
Paraonidae sp. 1 — 32.63	32.76	1.03	7.99	17.01
Oligochaeta — **15.5**	**62.64**	**1.47**	**7.41**	**24.42**
***Exogone* sp. 1** — **3.87**	**19.93**	**1.64**	**5.01**	**29.43**
Nucula hartvigiana — 12.33	10.29	1.24	4.13	33.56
Protophoxus australis — 5.67	11.13	1.29	3.94	37.5
Paracalliope novizealandiae — 3.53	10.73	1.18	3.62	41.12
Paracorophium excavatum — 3.87	10.87	0.64	2.97	44.09
Puyseguria turneri — 6.8	1.62	0.95	2.96	47.05
Capitellidae sp. 1 — 0.77	6.24	1.12	2.9	49.96

was slightly lower (48/49%) than that for assemblages of the shrimp/seagrass groupings. Taxa that contributed the most (6–12%) to the dissimilarities observed between the treatments/treatment groupings were somewhat similar (Table 4). Of the taxa that contributed the most to the dissimilarities observed, six taxa were particularly good at discriminating between the treatments/treatment groupings. In summer, these discriminating taxa included the amphipod crustaceans *Grandidierella japonica*, *Corophium acherusicum*, the spionid polychaetes *Streblospio benedicti* (all more abundant in seagrass treatment/treatment groupings),

Pygospio elegans and oligochaetes (both more abundant in shrimp treatments) for the dissimilarities in assemblage composition observed between shrimp/seagrass treatments/treatment groupings. *Corophium acherusicum* and *Pygospio elegans* were similarly discriminating taxa during winter, but during this season *Grandidierella japonica* was more abundant in the shrimp treatment grouping, as was another corophiid amphipod, *Corophium insidiosum*.

Taxa that best discriminated between high- and low-density treatments in summer for shrimp were *Grandidierella japonica* and *Corophium*

Table 4 Results from SIMPER analysis including mean abundance (α) and dissimilarity (DS) of macrofauna taxa averaged between significantly different treatments for summer and winter in the USA the ratio ($\bar{\delta}i/SD\delta i$) the percentage ($\delta i\%$) and cumulative percentage contribution ($\Sigma\delta i\%$) to the average Bray-Curtis dissimilarity between treatment groupings (cut-off to taxa list applied at 50% cumulative contribution to dissimilarity; those taxa with a ratio >1.3 are highlighted in bold)

USA

	Summer				
(α_S=hS α_Z=hZ&Mix)					
DS=57.72%	α_S	α_Z	$\bar{\delta}i/SD\delta i$	$\delta i\%$	$\Sigma\delta i\%$
Grandidierella japonica	**34.67**	**54.73**	**1.49**	**10.10**	**10.10**
Leptochelia savignyi	21.93	35.1	0.75	9.10	19.10
Pygospio elegans	17.07	25.07	1.20	8.58	27.67
Oligochaeta	**20.33**	**16.03**	**1.41**	**7.99**	**35.66**
Corophium acherusicum	**4.87**	**16.23**	**1.57**	**7.85**	**43.51**
(α_S=IS α_Z=hZ&Mix)					
DS=58.44%					
Grandidierella japonica	42.13	54.73	1.28	11.69	11.69
Oligochaeta	**34.40**	**16.03**	**1.36**	**9.01**	**20.69**
Pygospio elegans	8.67	25.07	1.11	7.37	28.07
Leptochelia savignyi	2.47	35.10	0.59	6.76	34.83
Streblospio benedicti	**11.27**	**22.70**	**1.44**	**6.71**	**41.54**
Corophium acherusicum	11.73	16.23	1.17	5.68	47.21
(α_S=hS α_Z=IZ)					
DS=57.43%					
Corophium acherusicum	**4.87**	**25.40**	**1.93**	**10.12**	**10.12**
Grandidierella japonica	**34.67**	**42.93**	**1.44**	**9.27**	**19.4**
Oligochaeta	**20.33**	**12.6**	**1.48**	**7.58**	**26.97**
Pygospio elegans	**17.07**	**15.4**	**1.32**	**7.01**	**33.99**
Capitella capitata	3.60	19.27	0.95	6.97	40.96
Streblospio benedicti	**12.33**	**18.13**	**1.32**	**6.85**	**47.81**
(α_{hS}=hS α_{IS}=IS)	α_{hS}	α_{IS}			
DS=61.98%					
Grandidierella japonica	**34.67**	**42.13**	**1.40**	**12.29**	**12.29**
Oligochaeta	20.33	34.40	1.22	10.92	23.21
Pygospio elegans	17.07	8.67	1.06	8.33	31.54
Pseudopolydora kempi	4.60	11.73	1.30	6.76	38.30
Corophium acherusicum	**4.87**	**11.73**	**1.45**	**6.35**	**44.66**
(α_{hZ}=hZ α_{IZ}=IZ)	α_{hZ}	α_{IZ}			
DS=47.60%					
Streblospio benedicti	**29.53**	**18.13**	**1.41**	**8.18**	**8.18**
Hobsonia florida	25.4	4.07	0.95	7.91	16.09
Leptochelia savignyi	31.27	2.87	0.73	7.54	23.63
Grandidierella japonica	**58.47**	**42.93**	**1.39**	**7.30**	**30.94**
Capitella capitata	2.13	19.27	0.98	7.10	38.04
Sinelobus stanfordi	1.40	14.2	0.94	6.03	44.07
Pygospio elegans	**12.80**	**15.4**	**1.36**	**5.92**	**49.99**
(α_{IZ}=IZ α_{Mix}=Mix)	α_{IZ}	α_{Mix}			
DS=48.94%					
Pygospio elegans	**15.40**	**37.33**	**1.34**	**9.29**	**9.29**
Capitella capitata	19.27	4.27	0.94	7.67	16.96
Streblospio benedicti	**18.13**	**15.87**	**1.43**	**7.35**	**24.3**
Grandidierella japonica	**42.93**	**51.00**	**1.37**	**7.34**	**31.65**
Leptochelia savignyi	2.87	39.93	0.59	7.21	38.85
Sinelobus stanfordi	1.42	5.67	0.90	6.76	45.61

Table 4 continued

USA

	Winter				
(α_S=IS&hS α_Z=hZ&Mix) DS=51.50%	α_S	α_Z			
Corophium acherusicum	**19.70**	**26.50**	**1.32**	**8.77**	**8.77**
Streblospio benedicti	18.37	47.23	1.20	8.56	17.33
Grandidierella japonica	**30.87**	**28.97**	**1.41**	**7.16**	**24.50**
Oligochaeta	18.00	18.40	1.14	6.67	31.16
Pygospio elegans	**17.23**	**10.00**	**1.31**	**6.26**	**37.42**
Leptochelia savignyi	4.47	22.67	0.73	6.14	43.56
Corophium insidiosum	**11.67**	**5.37**	**1.37**	**5.27**	**48.83**

acherusicum (both more abundant in low-density treatments), and for seagrass were the former amphipod, *Streblospio benedicti* (both more abundant in high-density treatment) and *Pygospio elegans* (more abundant in low-density treatment). The aforementioned spinoid polychaetes and *Grandidierella japonica* were discriminating taxa for low-density seagrass and mixed treatments in summer (*Streblospio benedicti* was more abundant at the low-density seagrass treatment sites, and the converse was true for the other two species).

BVSTEP analysis indicated which of the measured environmental variables (or combination) best explained the pattern of macrofauna assemblage composition observed for the two regions for both seasons (Table 5). In New Zealand in summer, the amount of seagrass debris was the environmental variable that alone best explained the pattern observed, whilst debris and % fines together produced the best overall correlation between environmental variables and assemblage composition. In winter, % fines alone had the best explanatory power. In the U.S.A., the single environmental variable that consistently ex-

plained the assemblage patterns observed in both seasons was the % carbon in the sediment. In summer, the overall correlation was highest with % carbon in conjunction with sediment turnover and % fines, whilst in winter the best correlation with assemblage composition was with % carbon and % fines. For both seasons, correlation coefficients were higher for New Zealand (ρ_w = 0.486–0.564) than for the U.S.A. (ρ_w = 0.296–0.435) data, indicating greater explanatory power of the measured environmental variables for the macrofauna assemblage composition observed in the former region.

An MDS ordination of macrofauna abundance data from New Zealand/winter superimposed with values of % fines illustrates how generally the environmental variables explained differences between locations and treatments (Fig. 3). That is, whilst there were noticeable differences in environmental variables between locations, there were also differences in the environmental variables between treatments. For the latter differences, values of % fines, % carbon and debris were generally higher for seagrass treatment than for shrimp treatment sites (Table 6).

Table 5 Results of BVSTEP stepwise analysis indicating which combination of the measured environmental variables best explains the pattern of macrofauna assemblage composition observed for each region/season and which individual variable contributes the most to the correlation coefficient (ρ_w)

	Summer		Winter	
	Best variable(s)	ρ_w	Best variable(s)	ρ_w
New Zealand	Debris	0.486	% Fines	0.502
	Debris, % Fines	0.564		
U.S.A	% C	0.296	% C	0.397
	% C, Sediment turnover, % Fines	0.382	% C, % Fines	0.435
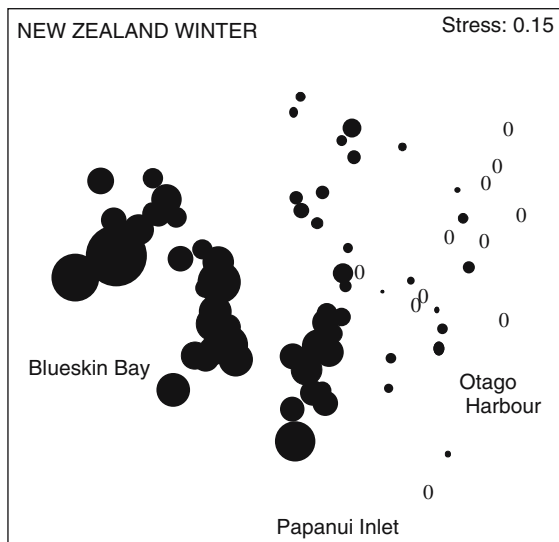
Fig. 3 MDS ordinations of infaunal macrofauna abundance data (square-root-transformed) from treatment sites at locations in New Zealand in winter with superimposed cricles representing % fines of sediment grain size (circle size is proportional to increasing % fines, 0 = zero % fines)

Discussion

Findings from our study confirmed the importance of burrowing ghost shrimps and seagrasses in regards to influencing the composition of benthic assemblages, and revealed a generality in the ecosystem engineering capacity of these two species across locations and regions in the temperate zone. In New Zealand and the U.S.A., both the allogenic and autogenic types of ecosystem engineer consistently influenced associated sediment infauna, and shrimp and seagrass treatment sites within the study estuaries/tidal inlets were characterised by distinct macrofauna assemblages, evident in summer and winter.

Previous studies have documented the ecological significance of either bioturbating shrimps or seagrasses in relation to soft-sediment communities. The importance of bioturbating shrimps has been established in ecological studies that examined associated faunal communities in relation to shrimp density in temperate systems (Tamaki and Kikuchi 1983). Densities of most common taxa have been shown by several authors to be greatly reduced in areas where *Neotrypaea californiensis* is highly abundant (100 shrimp/m^2) in Pacific

Northwest/United States estuaries (Posey 1986; Dumbauld et al. 2001; Ferraro and Cole 2004). Similarly, naturally occurring differences in *Callianassa filholi* abundance in New Zealand were reflected in distinct community differences, even though density levels were much lower than those of its North American counterpart (1–10 shrimp/m^2; Berkenbusch et al. 2000).

Seagrass beds have received considerable attention as temperate coastal habitats that support significantly higher number of species and individuals than unvegetated areas (Stoner 1980; Orth et al. 1984; Boström and Bonsdorff 1997). This perception has been supported by studies on *Zostera capricorni* in New Zealand, which showed generally higher species abundance and diversity inside seagrass patches than in bare sediment (Henriques 1980; Turner et al. 1999). The influence of *Zostera japonica* on associated macrofauna has been evidenced in Oregon and in its native range in Hong Kong (People's Republic of China), where transplanted and naturally established *Zostera japonica* patches showed a significant effect on benthic assemblages through a marked increase in common taxa and species abundance when compared to bare sediment (Posey 1988; Lee et al. 2001). These studies identified ghost shrimps and seagrasses as important structuring agents per se, but there has been little information regarding their interactions in determining assemblage composition.

The present study of two types of ecosystem engineering species at different spatial and temporal scales allowed for an exploration of possible interactions between such engineers and the potential underlying mechanisms by which ghost shrimps and seagrasses, in particular, exert their influence. Previous studies that directly examined the interactions between burrowing ghost shrimps and seagrasses have shown different adverse effects between the two types of ecosystem engineers in tropical and temperate regions (Roberts et al. 1981; Suchanek 1983; Harrison 1987). The abundance and productivity of several seagrass species in tropical lagoons (U.S. Virgin Islands) were negatively correlated with *Callianassa* spp. mound density (Roberts et al. 1981; Suchanek 1983). Furthermore, experimental transplantation of seagrass into areas of high mound density

Table 6 Mean values (±SE) of environmental parameters indicated by BVSTEP analysis that best explain differences in macrofauna assemblage composition in each region and season (All values per 78.5 cm² except sediment turnover which was based on mean values from 3 traps per treatment site)

New Zealand		Otago Harbour % Fines	Seagrass debris (g)	% C	Blueskin Bay % Fines	Seagrass debris (g)	Papanui Inlet % Fines	% C	Seagrass debris (g)
Summer	hS	0.45±0.45	0.66±0.42	0.48±0.13	9.23±1.99	5.21±0.79	4.14±0.52	0.68±0.10	0.27±0.15
	IS	1.46±0.90	0.66±0.52	1.61±0.34	8.24±0.74	6.47±1.00	4.47±0.30	0.61±0.26	2.01±1.03
	hZ	4.09±0.22	2.92±0.67	1.00±0.21	8.20±0.87	3.61±0.96	10.44±1.31	0.69±0.03	1.67±0.20
	IZ	1.80±0.64	0.81±0.18	1.24±0.33	7.79±0.81	5.90±1.27	8.14±0.31	0.62±0.02	1.56±0.16
	Mix	2.80±0.23	1.57±0.55	0.77±0.15	9.90±0.57	5.96±0.54	7.16±0.74	0.64±0.04	1.89±0.54
Winter	hS	0.26±0.26	0.52±0.31	0.53±0.18	8.74±2.38	1.39±0.41	3.35±0.51	0.84±0.12	0.32±0.18
	IS	0.59±0.59	0.75±0.53	1.53±0.28	9.37±1.19	2.00±0.23	3.53±0.24	1.00±0.26	1.08±0.23
	hZ	2.00±0.55	1.48±0.39	0.91±0.14	9.01±1.09	1.87±0.18	8.90±0.83	0.77±0.01	2.76±0.44
	IZ	2.18±0.67	1.11±0.33	1.12±0.29	9.57±0.92	2.35±0.22	7.47±0.73	0.75±0.03	2.04±0.38
	Mix	1.19±0.61	0.71±0.14	0.62±0.18	8.22±0.83	1.79±0.29	6.03±0.46	0.66±0.04	1.64±0.36

USA		Tillamook Bay % Fines	% C	Sediment turnover (g)	Yaquina Bay % Fines	% C	Sediment turnover (g)	Netarts Bay % Fines	% C	Sediment turnover (g)
Summer	hS	15.68±3.52	0.48±0.13	48.31±2.84	10.93±1.33	0.68±0.10	7.61±3.71	10.81±2.15	0.30±0.05	5.80±2.44
	IS	68.31±10.21	1.61±0.34	5.55±1.79	16.64±1.64	0.61±0.26	3.65±0.72	6.57±1.54	0.17±0.01	2.56±0.91
	hZ	40.99±7.89	1.00±0.21	0.00±0.00	16.74±4.85	0.69±0.03	0.00±0.00	6.73±1.03	0.17±0.02	0.00±0.00
	IZ	55.27±7.46	1.24±0.33	0.00±0.00	14.69±1.37	0.62±0.02	0.00±0.00	9.40±2.34	0.25±0.06	0.00±0.00
	Mix	40.72±9.75	0.77±0.15	8.91±5.10	12.93±0.78	0.64±0.04	4.18±1.85	5.21±0.42	0.17±0.02	4.31±0.13
Winter	hS	26.44±9.40	0.53±0.18	1.47±0.92	7.88±0.61	0.84±0.12	1.36±0.53	10.11±0.68	0.35±0.03	0.50±0.35
	IS	74.67±8.50	1.53±0.28	0.13±0.09	9.60±1.21	1.00±0.26	0.33±0.13	8.11±1.02	0.20±0.01	1.66±0.73
	hZ	43.30±5.38	0.91±0.14	0.00±0.00	9.53±0.53	0.77±0.01	0.00±0.00	7.41±1.34	0.23±0.04	0.00±0.00
	IZ	56.82±8.15	1.12±0.29	0.00±0.00	8.73±0.55	0.75±0.03	0.00±0.00	7.79±2.08	0.24±0.06	0.00±0.00
	Mix	36.13±9.57	0.62±0.18	0.32±0.15	8.08±0.37	0.66±0.04	0.43±0.21	7.32±1.14	0.24±0.05	2.19±0.38

showed physical deterioration of seagrass blades within 2 weeks, followed by a dramatic decline in overall plant density within 2–4 months (Suchanek 1983). In contrast, Harrison (1987) observed in a temperate system (British Columbia, Canada) that *Neotrypaea californiensis* temporarily declined in areas where *Zostera japonica* shoots had been experimentally added, whilst the ghost shrimp rapidly colonised sites where the seagrass had been removed. Negative effects arising from burrowing ghost shrimps may be due to burying of seeds, physical smothering of adult plants, and reduced light levels which inhibit photosynthesis (Suchanek 1983; Duarte et al. 1997; Dumbauld and Wyllie-Echeverria 2003). At the same time, dense seagrass root-rhizome mats may impede burrowing by adult shrimp and settlement of juveniles (Brenchley 1982; Harrison 1987). In areas where ghost shrimp and seagrass populations are naturally interspersed, populations of either type of organism appear to persist at intermediate threshold densities beyond which they cannot expand until the environment is disturbed in a way that favours one of the species (Harrison 1987). The successful expansion of either ghost shrimp or seagrass following a natural (e.g., storm, disease) or anthropogenic (e.g., harvesting, pollution) disturbance appears to depend on seasonal timing, where a competitive advantage is provided for seagrasses in spring (time of maximum growth) and for ghost shrimp in summer (time of peak activity in sediment turnover) (Harrison 1987).

Of the environmental variables that explained the assemblage composition differences observed during the present study, sediment % fines, % carbon and seagrass debris implicated seagrass as the dominant ecosystem engineer, and indicated why the composition of assemblages at seagrass and mixed treatment sites were similar. The generally higher values for % fines and % carbon at seagrass treatment sites were most likely due to seagrass leaves baffling currents and reducing flow velocities, thereby creating an environment of enhanced deposition for fine sediment and organic particles (Grady 1981; Fonseca and Fisher 1986). At the same time, the relative lack of sediment reworking by ghost shrimps at seagrass sites meant that organic matter would remain

available at the top of the sediment rather than being processed by shrimp (Stamhuis et al. 1998; Stapleton et al. 2001). A high proportion of fine particles in the top layer of the sediment represented sediment grains with a high surface to volume ratio, which is advantageous for bacterial growth and accumulation of organic matter on the grain surface (Taghon 1982; Levinton 1995). Percent carbon is a direct reflection of the amount of organic matter within the sediment, and it is therefore likely that both sediment parameters are important to episammic animals for nutritional reasons (Little 2000). In particular deposit-feeding infauna are likely to benefit from an increased food supply in seagrass areas (Boström and Bonsdorff 1997) and therefore increased food availability might explain the high relative abundance of amphipod crustaceans (i.e. *Corophium acherusicum*, *Grandidierella japonica*, *Protophoxus australis*), deposit feeding polychaetes (*Aquilaspio aucklandica*, *Streblospio benedicti*) and oligochaetes (New Zealand only) observed at seagrass compared to shrimp sites.

Interactions between infauna and seagrasses have previously been shown to be positive, with much higher densities of *Corophium* spp., *Streblospio benedicti*, and oligochaetes observed in *Zostera japonica* or *Z. capricorni* vegetated areas than unvegetated areas, differences that corresponded to higher values of fine particles and volatile organics in seagrass patches compared to bare areas (Posey 1988; Turner et al. 1999). The ability of amphipods to rapidly colonise artificial seagrass patches from a distance of several metres demonstrates their particular aptitude to actively seek out a favourable habitat (e.g. *Grandidierella* sp., Virnstein and Curran 1986). Whilst it has been suggested that high-density seagrass sites exclude relatively large deposit feeding amphipods and polychaetes because dense roots and rhizomes prevent burrowing into the sediment (Stoner 1980; Brenchley 1982; Webster et al. 1998), the prevalence of deposit feeders such as *Corophium acherusicum*, *Aquilaspio aucklandica* and *Streblospio benedicti* at seagrass sites of the present study indicates that these species are not necessarily restricted by seagrass below-ground material. The inconsistent abundance pattern for oligochaetes in Oregon, i.e. relatively high

numbers at ghost shrimp sites in summer, corresponded with markedly higher values for sediment % fines at low- or high-density shrimp sites in comparison to seagrass treatments in this region. It is, therefore, likely that aforementioned populations would respond to the increased availability of suitable food material, which generally characterised seagrass sites in both regions.

The particular significance of seagrass debris for macrofauna at the New Zealand locations during summer may also be related to the provision of food, either directly or through bacterial growth. Plant material can be utilised directly by herbivores and detritus feeders (Jernakoff and Nielsen 1997), whilst the release of gases and photosynthates affects microbial processes and bacterial growth on the plant matter with trophic flow-on effects for larger-sized organisms (Penhale and Smith 1977; Luczkovich et al. 2002). The decomposition of senescent seagrass material impacts on nutrient cycling and retention, which affects the food availability for meio- and subsequently macrofauna (Castel et al. 1989; Kharamenko et al. 2001), in particular during summer, when bacterial growth is most prolific. Consistently higher oligochaete densities at *Zostera capricorni* sites in New Zealand support this notion, because oligochaetes are opportunistic feeders that can utilise decaying seaweed and seagrass, and have been shown to ingest algal thalli and *Zostera marina* leaves from wrack beds (Giere and Pfannkuche 1982). Lee et al. (2001) examined faunal communities in relation to *Zostera japonica* within its native range in Hong Kong and found that species abundance and richness of both epi- and infauna assemblages were positively related to below-ground seagrass biomass and to detritus (seagrass and macro-algae), which they also attributed to an increase in food supply. In contrast, negative effects associated with seagrass debris could be related to the impediment of movement and unfavourable biogeochemical conditions through the decomposition of senescent seagrass material, which would influence macrofauna abundance patterns. In New Zealand, the polychaete *Paraonidae* sp. 1 and the small bivalve *Perrierina turneri* were more abundant at shrimp than seagrass treatment sites. Members of the Paraonidae are adapted to

living at the sediment surface (Rouse and Pleijel 2001), and seagrass debris and fine sediment particles reduce porosity and increase compaction (Little 2000), which in turn may impede this taxon's mobility which could explain the pattern of relative abundance of these polychaetes observed in the present study. Bird (1982) postulated that positive effects of *Neotrypaea californiensis* on free-burrowing amphipods were associated with an increase in sediment permeability, because such amphipods are adapted to burrowing through loose substrate, but excluded from compacted sediment for energetic reasons.

A similar underlying mechanism might explain the high abundance of *Perrierina turneri* observed at *Callianassa filholi* sites compared to sites that contained *Zostera capricorni*. This abundance pattern is surprising, as a number of studies have demonstrated the adverse effects of ghost shrimp bioturbation on small-sized bivalves, where the associated increased turbidity and de-stabilisation of sediment have been linked to inhibited recruitment, growth and survival of suspension-feeding bivalves (Myers 1977; Peterson 1977; Murphy 1985). In a previous study conducted in Otago Harbour in New Zealand, *Perrierina turneri* numbers were higher at low-density than at high-density ghost shrimp sites, a finding that was attributed to the relative bioturbation activity of *Callianassa filholi* (Berkenbusch et al. 2000). In the aforementioned study, total seagrass biomass was considerably lower than in the present one, and it is possible that for *Perrierina turneri* the adverse effect of seagrass debris prevailed over that of ghost shrimp bioturbation to the extent that the bivalve was able to be more abundant at *Callianassa filholi* high-density sites, where less seagrass debris was present.

Sediment turnover by ghost shrimp contributed to the explanation for the observed assemblage composition differences in the U.S.A. region during summer. The marked increase in ghost shrimp activity in this season is likely to affect species that are susceptible to bioturbation, but which might be able to tolerate lower levels of sediment disturbance during winter. Amphipods, in particular tube-building corophiids, have a demonstrated susceptibility to bioturbation, which excludes them from ghost

shrimp sites at times of high sediment turnover activity (Bird 1982; Posey 1986; Berkenbusch et al. 2000). This previous observation could explain why *Grandidierella japonica* and *Corophium insidiosum* in the present study exhibited high densities at seagrass sites in summer and at shrimp sites during winter. The spionid polychaete *Pygospio elegans* also demonstrated the same pattern of relative abundance between treatment sites by season and could thus be similarly affected by (and respond to) high levels of sediment turnover activity. The prevalence of this species at mixed treatments in summer indicates that *Pygospio elegans* can tolerate bioturbation to a certain extent. The resilience of this species to a degree of sediment disturbance has been linked to the creation of a dense tube-matrix that can prevent sediment erosion and thereby compensate for shrimp bioturbation (Boström and Bonsdorff 2000).

Most discriminating taxa generally showed a strong prevalence for treatment sites that contained seagrass, implying that seagrass is the dominant ecosystem engineer in the systems studied. However, the exploration of biological and environmental data from both regions indicated that the response of individual taxa within assemblages was based on positive and negative effects, or the combination of both, arising from the presence of bioturbating shrimps and/or seagrasses. These findings are in accordance with Jones et al. (1997), who suggested that only some species benefit from the engineered ecosystems, whereas others are negatively affected by the presence and activity of physical ecosystem engineers. Furthermore, interactions between shrimps and seagrasses revealed by the present study provide a case example of what Jones et al. (1997) called "multiple engineers and coupled and uncoupled trophic interactions". The assemblage composition of intertidal infauna, in soft-sediment areas of temperate estuaries/tidal inlets where both shrimp and seagrass co-exist, is thus likely to be in dynamic equilibrium (Huston 1979) as a direct or indirect result of bioturbation and organic enrichment perpetrated by these
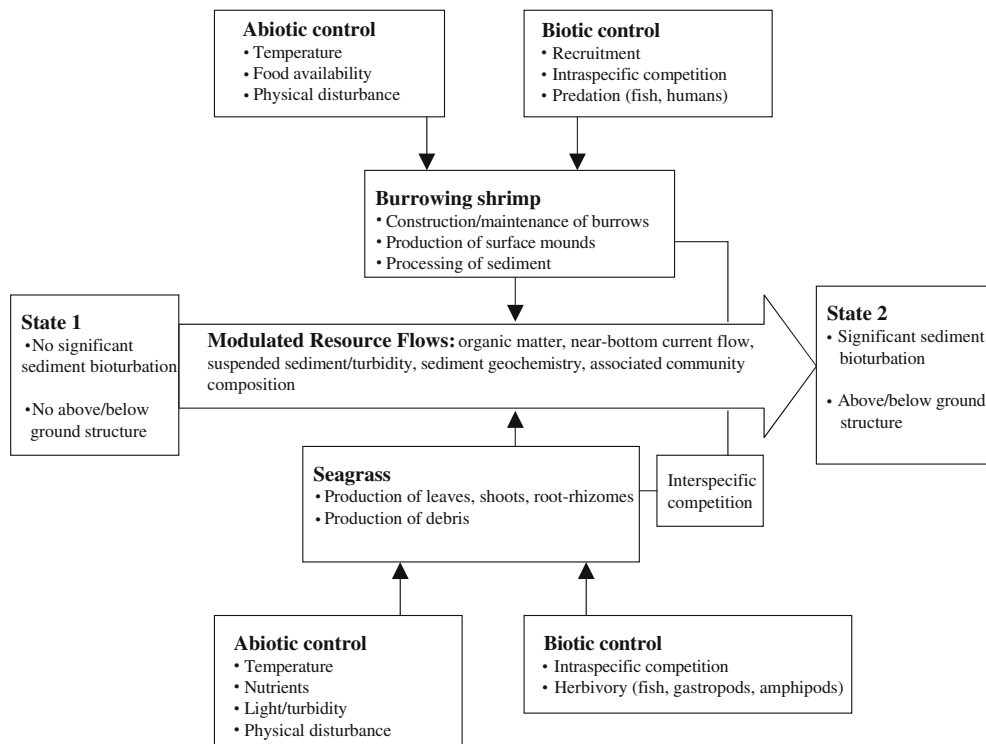
Fig. 4 Conceptual model of ecosystem engineering by burrowing shrimp and seagrass in intertidal habitats

ecosystem engineers. Evidence for the interaction of the same structuring forces in determining (sub-tidal) soft-sediment assemblage composition has been shown previously (Widdicombe and Austen 2001). Thus, the present study helps to establish how engineering species that co-exist in the same type of habitat generally influence structuring forces and processes that determine the composition of assemblages. In particular, the study has allowed for the further development of a conceptual model of how burrowing shrimp and seagrass act as ecosystem engineers in intertidal soft sediment habitat (Fig. 4).

This heuristic model (modified after Berkenbusch and Rowden 2003) for ecosystem engineering by seagrass and shrimp illustrates that, whilst creating a related numerical model would be desirable as a means to further investigate the concept, constructing and parameterising a model with such a multitude of influences and interactions would be a complicated. Gurney and Lawton (1996) presented three more tractable mathematical models involving a single species of engineer and the habitat they modify, demonstrating their usefulness for exploring the concept of ecosystem engineering. The present study reveals that at least a fourth type of model is required, one that involves two species of co-occuring ecosystem engineers. Furthermore, considering that populations of shrimp and seagrass are in-part maintained by physical and stochastic forces with a spatial component (e.g. seasonal current regime changes and mass sediment transport by large periodic storms; Fonseca and Bell 1998; Preen et al. 1995), it will be necessary to construct spatially and temporally explicit models. In order to effectively construct such models, studies will need to be conducted to obtain field data that specifically examine, at multiple spatial and temporal scales, the population-level interaction between shrimps and seagrass, particularly to establish the existence of presumed density-dependant relationships. Manipulative experimentation to determine whether the likely mechanisms identified by the present mensurative study are indeed the causes of the observed patterns are necessary to further elucidate their effects on the composition of associated assemblages.

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