

Interactions between seagrasses and burrowing ghost shrimps and their influence on infaunal assemblages

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Abstract

The current study examined the direct interactions between intertidal seagrasses (*Zosteraceae*) and burrowing ghost shrimps (*Callianassidae*) and their influence on associated infaunal assemblages. Reciprocal transplant experiments conducted in two temperate regions revealed different interactions between both types of organism. In the U.S.A., seagrass prospered in all treatments, irrespective of the presence of ghost shrimp, whilst ghost shrimp declined in plots containing seagrass. In New Zealand, neither transplanted ghost shrimp nor seagrass became established in experimental plots, at the same time, neither type of organism appeared to be affected by the experimental addition of transplants. The differences in interactions between seagrass and ghost shrimp appeared to be related to seasonal differences in the timing of the transplant experiments and the pairing of particular ghost shrimp and seagrass species in each region. Infaunal assemblages showed distinct differences between seagrass and ghost shrimp treatments and reflected the dominant type of organism present. In treatments where transplanted seagrass or ghost shrimp became established, assemblage composition shifted in accordance with the type of transplanted organism. Differences in assemblage composition were characterised by higher relative abundances of discriminating taxa in treatments dominated by seagrass. The overall patterns of infaunal assemblage composition were correlated with a number of variables including the number of shoots, above-, below-ground seagrass biomass, % fines/sand, % total organic carbon, and sediment chlorophyll *a*. Findings from this study highlight the functional importance of intertidal seagrasses and burrowing ghost shrimps and reveal some of the ecological repercussions associated with changes in the distribution of these sympatric ecosystem engineers.

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1. Introduction

Marine communities frequently contain organisms that have a disproportionate influence on associated species

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and ecosystem functioning (ecosystem engineers, Levinton, 1995; Bouma et al., 2005; Gutiérrez and Jones, 2006). In sedimentary coastal habitats, burrowing ghost shrimps (i.e., members of the *Callianassidae*) and seagrasses (e.g., *Zosteraceae*) play a significant role as ecosystem engineers that regulate community composition and ecological processes (Fonseca and Fisher, 1986; Berkenbusch et al., 2000; Thomas et al., 2000; Contessa and Bird, 2004). Burrowing and deposit-feeding by ghost shrimps affect the geo-technical and biogeochemical

properties of the sedimentary environment, including sediment grain size, nutrient exchange and organic decomposition (Tudhope and Scoffin, 1983; de Vaugelas and Buscail, 1990; Ziebis et al., 1996; Webb and Eyre, 2004). Furthermore, ghost shrimp bioturbation can lead to significant sediment turnover and re-suspension, promoting sediment erosion and instability (de Vaugelas, 1985; Aller and Dodge, 1974; Rowden et al., 1998). Biological implications of these habitat modifications include both beneficial and adverse effects for associated flora and fauna, and the functional importance of burrowing ghost shrimps has been highlighted in ecological studies of benthic communities (Suchanek, 1983; Posey, 1986; Dittmann, 1996; Berkenbusch et al., 2000; Dumbauld and Wyllie-Echeverria, 2003).

Seagrasses play a vital role in the function of coastal habitats through the provision of structure, their high productivity, and contribution to detrital food chains (Christian and Luczkovich, 1999; Kharlamenko et al., 2001; Spalding et al., 2003; Moore et al. 2004). Through above- and below-ground structure (leaves and root–rhizome matrix), seagrass beds directly provide habitat, shelter and food, and influence sedimentation rates, enhancing the accumulation of relatively high organic particulates (Leber, 1985; Fonseca and Fisher, 1986; Castel et al., 1989). The structural complexity of seagrass beds has been highlighted as an important factor determining the composition of benthic communities, and biological flow-on effects include the increase in species abundance and diversity in seagrass habitats compared to unvegetated sediments (Heck et al., 1995; Bostrom and Bonsdorff, 1997; Connolly, 1997; Turner and Kendall, 1999).

Whilst the ecological significance of ghost shrimps and seagrasses has been widely recognised, there is relatively little information regarding their direct interactions with each other. This is particularly relevant, as both types of organisms are common in tropical and temperate ecosystems where they frequently co-occur in the same habitat (Roberts et al., 1981; Harrison, 1987; Posey, 1987; Berkenbusch et al., 2000; Siebert and Branch, 2005).

Studies that have examined the natural distribution of sympatric seagrass and ghost shrimp in the Tropics revealed a negative correlation between seagrass abundance and biomass in relation to ghost shrimp mound density (Roberts et al., 1981; Suchanek, 1983). In addition, artificially established seagrass (predominantly *Thalassia testudinum*) plots at high-density ghost shrimp (*Callianassa* sp.) sites deteriorated dramatically within weeks of transplantation, demonstrating the ability of callianassid shrimps to control seagrass

distribution and abundance in shallow Caribbean lagoons (Suchanek, 1983). The mechanisms by which ghost shrimps exert their negative influence are likely linked to the direct effects of sediment disturbance, causing the physical displacement and burial of seagrass plants, seeds and/or seedlings (Suchanek, 1983; Duarte et al., 1997; Dumbauld and Wyllie-Echeverria, 2003). Indirect adverse effects arising from ghost shrimp bioturbation might be linked to the impediment of photosynthetic processes as increased sedimentation and resuspension of fine particles reduce available sunlight and cover seagrass blades in silt (Suchanek, 1983).

In the temperate region, seagrasses have been shown, conversely, to negatively affect the abundance of ghost shrimp. In British Columbia (Canada) the ghost shrimp *Neotrypaea californiensis* showed a sharp population decline in areas that had been invaded by the seagrasses *Zostera marina* and *Z. japonica* over a period of 8 years (Harrison, 1987). Furthermore, transplantation of *Z. japonica* shoots into ghost shrimp areas led to a temporary decrease in *N. californiensis* abundance, whilst experimental removal of seagrass resulted in the recruitment of ghost shrimp to denuded sites (Harrison, 1987). In a laboratory setting, *N. californiensis* appeared to be unable to penetrate sediment that included dense roots and rhizomes of *Z. marina*, and it has been suggested that the root–rhizome matrix of seagrasses impedes mobility, particularly burrowing of large infauna such as ghost shrimp (Brenchley, 1982). Thus to date, studies that have assessed the interactions between ghost shrimps and seagrasses document the ability of either type of organism to significantly impact upon the other, resulting in the formation of largely monospecific beds.

The proximity of high-density seagrass and ghost shrimp beds appears to confirm the suitability of the same intertidal habitat for both types of organisms. At the same time that high-density ghost shrimp beds frequently border on dense seagrass meadows, the presence of mixed areas where ghost shrimp and seagrass populations are present at lower densities indicates that there is an apparent threshold density level at which both types of organism can co-exist (Harrison, 1987; Siebert and Branch, 2005). Whilst it remains unclear exactly what determines the predominance of either seagrass or ghost shrimp in habitats that seem suitable for both, it has been speculated that the successful population expansion of either organism is dependent on a disturbance event that upsets an apparently precarious balance (Harrison, 1987). The timing of such disturbance, for example in the temperate region, may favour a seagrass population in spring, at a

time of maximum growth, and ghost shrimps during summer when bioturbation reaches a peak (Harrison, 1987). After disturbance by severe storms (cyclones) in tropical regions, ghost shrimp bioturbation rates can return to pre-storm levels in a relatively short time (weeks) (Riddle, 1988). However, it is possible where seagrass exists in the same area, its surviving population may expand during the ghost shrimp recovery period.

In view of the recently established ecological importance of seagrasses and burrowing ghost shrimps where they occur in the same habitat (by mensurative experiments; Berkenbusch et al., 2000; Berkenbusch and Rowden, in press), and their inclusion in developing heuristic models of ecosystem function (Berkenbusch and Rowden, 2003, in press), it is important to better resolve the factors that determine the abundance and distribution of both types of ecosystem engineers and to elucidate the possible mechanisms by which these species influence the composition of associated infaunal assemblages. Thus, the present study aimed to examine the direct interaction between temperate ghost shrimps and seagrasses through reciprocal transplant experiments and the consequences of such an interaction for the infauna of the same intertidal habitat.

2. Materials and methods

2.1. Study sites and organisms

Manipulative experiments were conducted in two temperate regions, north-western U.S.A. and south-eastern New Zealand. In each region, an estuary/tidal inlet was selected that contained burrowing ghost shrimp and seagrass within the same intertidal area. Both estuaries were similar in size, shape, tidal range and general sediment characteristics (see Berkenbusch and

Rowden, in press); they were Netarts Bay in the U.S.A. and Papanui Inlet in New Zealand (Fig. 1).

Burrowing ghost shrimp species in this study were *N. californiensis* (Dana, 1854) and *Callianassa filholi* Milne-Edwards, 1878 in the U.S.A. and in New Zealand, respectively. These species are similar in size (10–16 mm adult carapace length) (Dumbauld et al., 1996; Berkenbusch and Rowden, 1998); both are considered to be primarily deposit-feeders (Morton and Miller, 1968; Ricketts et al., 1985); they construct relatively extensive semi-permanent burrows (11–66 cm deep, lateral extent of 15–113 cm) that connect to the sediment surface by multiple openings (2–5), of which 1–3 terminate in mounds of expelled sediment (Swinbanks and Murray, 1981; Griffis and Chavez, 1988; Berkenbusch and Rowden, 2000); exhibit seasonal variation in bioturbation activity with high sediment turnover rates during summer (8–10 g and 30–60 g of sediment dry weight per mound per day for *N. californiensis* and *C. filholi*, respectively) and markedly lower values (c. 20%) during colder months (Berkenbusch and Rowden, 1999; Fritz, 2002; Berkenbusch and Rowden, in press); and are common in intertidal soft-sediment environments in their respective regions (mean density of 16 and 230 individuals m^{-2} , *C. filholi* and *N. californiensis*, respectively; Dumbauld et al., 1996; Berkenbusch and Rowden, 1998).

Corresponding seagrass species were *Z. japonica* Aschers. and Graebn, U.S.A., and *Z. capricorni* Asch., New Zealand. *Zostera japonica* is an introduced species to the Pacific coast of North America where it arrived from eastern Asia in the late 1800s (Harrison and Bigley, 1982), whilst *Z. capricorni* is native to New Zealand and Australia (Les et al., 2002). Both seagrass species are similar in size (approximately 20 cm average leaf length, 1 mm average leaf width) (Setchell, 1933; Bigley and

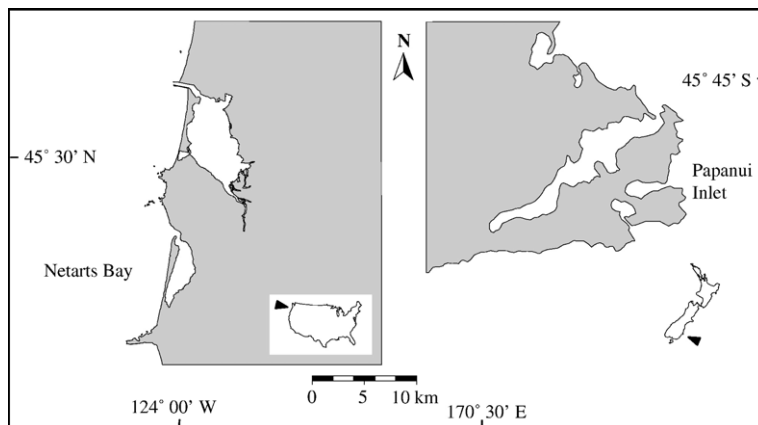


Fig. 1. Location of study sites in Netarts Bay/U.S.A and Papanui Inlet/New Zealand.

Harrison, 1986; Rampage and Schiel, 1999), relatively small in comparison to other seagrasses; create monospecific beds that vary in size from several m² to >10 km² (Bulthuis, 1995; Inglis, 2003; Larned, 2003); and are characterised by seasonal fluctuations in biomass, as shoot density and above-ground biomass increase over spring and summer (~7500–10,000 shoots/m²; 60–100 gDW/m²), and decline to minimum values in the middle of winter (~1500–5500 shoots/m²; 20–40 gDW/m²) (Ismail, 2001; Kaldy, 2006).

2.2. Experimental set-up

Within each estuary, treatment “sites” (ca. 4–9 m²) were arbitrarily chosen to each represent naturally occurring ghost shrimp or seagrass areas, where either type of organism was present at the lower end of its density range in monospecific beds (i.e., at densities near the presumed interaction threshold level). At each treatment site, bottomless buckets (0.066 m² surface area, 37 cm depth) were inserted into the sediment, so that the top of the bucket was level with the sediment surface. The buckets were used as “plots” and provided a lateral restriction for ghost shrimp movement and seagrass expansion, whilst enabling water movement across the sediment surface.

The experiment involved four treatments: (1) seagrass transplanted to ghost shrimp sites (Sh/Zo), (2) ghost shrimp transplanted to seagrass sites (Zo/Sh), (3) naturally occurring ghost shrimp sites (ShC), and (4) naturally occurring seagrass sites (ZoC). The latter two treatments were defined as controls, as it was impossible to locate areas at the study sites that contained neither type of organism into which transplants could be placed. The number of transplanted seagrass shoots and ghost shrimp was based on naturally occurring densities in each estuary, in areas where either type of organism was present. Each treatment was comprised of five haphazardly placed replicate plots, which were spread across the tidal range of the shrimp/seagrass sites.

Seagrass transplants consisted of individual shoots and associated roots that were carefully removed from adjacent seagrass beds, and gently washed in seawater to remove resident fauna. Shoots were subsequently planted into the top of the sediment of Sh/Zo transplant plots. Ghost shrimp for transplanting were collected from nearby shrimp areas using a suction pump, and medium-size individuals (7–8 mm carapace length) were placed on the sediment surface in Zo/Sh treatments. The number of ghost shrimp added to Zo/Sh treatments in both estuaries was higher than the target density, to account for an estimated 25% failure

rate of ghost shrimp to burrow within the first 24 h (Brenchley, 1982).

All treatment plots were covered with mesh (1 mm) for 24 h to monitor the initial success of the transplant over two tidal cycles. The number of dislodged shoots and ghost shrimp that had failed to burrow was recorded following the removal of the mesh.

Due to logistical constraints, it was not possible to conduct the transplant experiment in each region during exactly the same season. In Netarts Bay, the study was initiated on April 9, 2003 and terminated on August 29, 2003, encompassing the boreal spring to summer. Seagrass transplants consisted of sixty shoots and ghost shrimp transplants were comprised of 8 individuals per respective treatment. In Papanui Inlet, the field experiment was set up on January 16, 2004, and run until July 17, 2004, encompassing the austral summer to winter. In this estuary 120 seagrass shoots and 8 ghost shrimp were transplanted into the respective treatments. Each study site was monitored regularly (fortnightly in the U.S.A. and weekly in New Zealand) to assess the condition of transplants and to count the number of seagrass shoots and ghost shrimp mounds in each treatment plot. Ghost shrimp mound density was used as a non-destructive proxy measure of ghost shrimp abundance, which had been validated in a previous study (see Berkenbusch and Rowden, *in press*).

2.3. Sample collection and analysis

At the start and end of the experiment, seagrass, infauna, and sediment samples were collected from each treatment site. At the start of the study, sampling was conducted in an area directly adjacent to each bucket, whereas the final sampling occurred in the middle of each treatment plot.

Seagrass above-ground biomass was sampled by placing a plastic ring (10 cm \varnothing) on the sediment surface and cutting off all shoot material within it. Shoots and leaves were rinsed in freshwater, counted, dried (48 h at 60 °C) and weighed (± 0.0001 g). Infaunal samples were collected in the same area as seagrass by using a core (10 cm \varnothing , 10 cm depth) and sieving the content of each core on 500 μ m mesh. Retained invertebrates were preserved in 70% isopropyl alcohol with 0.2% Rose Bengal, identified to the lowest practical taxonomic level (generally species) and counted using microscopy. 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 infauna samples, rinsed in

freshwater, dried (48 h at 60 °C) and weighed (± 0.0001 g).

Sediment cores were taken for granulometry, organic content (same core 3 cm \varnothing , 10 cm depth) and chlorophyll *a* (2.5 cm, 2 cm depth) analysis, and kept frozen prior to laboratory analysis. In the laboratory, samples for sediment grain size were digested in 6% hydrogen peroxide for 24 h to remove organic matter. Sediment grain size was subsequently determined by laser diffraction particle size analysis, after samples were wet-sieved on 850 μm (Netarts Bay) and 500 μm (Papanui Inlet) mesh. Sieve sizes were dictated by the upper size limit of the respective laser diffraction particle size analyser used in each country, and the proportion of sediment retained on the sieve was included in the overall analysis (only applicable for Papanui Inlet samples).

Organic content was determined by loss of weight on ignition (4 h at 500 °C) after samples were dried to constant weight for 48 h. Sediment chlorophyll *a* was extracted by boiling a homogenised and freeze-dried sediment sub-sample (5 g) in 90% ethanol. The extract was analysed using a spectrophotometer, and included an acidification step to separate degradation products from chlorophyll *a* (Sartory, 1982).

Following the final sampling, the contents of each bucket were excavated and sieved on 3 mm mesh to ascertain the number of ghost shrimp in each treatment. Ghost shrimp retained on the mesh were anaesthetised (7.5% magnesium chloride in freshwater) for 5 h prior to fixation in 10% formalin/seawater, and subsequently counted.

2.4. Bioturbation rates

At both study estuaries, ghost shrimp bioturbation rates were assessed in an area adjacent to the transplant site and encompassing the same tidal range, at the start and end of the transplant experiment. Sediment expelled from burrows was trapped over a 24 h period by using plastic containers (11 cm \varnothing) with a 1 cm hole in the bottom and bolting mesh on top (110 μm) to prevent loss of sediment from the trap. In each estuary, thirty burrows were haphazardly selected, from which burrow mounds were carefully removed. Sediment traps were placed over the exposed burrow expulsion hole and secured with wire stakes. An equal number of control traps were deployed at the same time. 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 from displaced or damaged sediment traps were not included in subsequent analyses.

2.5. Data analysis

Differences in the number of shoots between treatments that contained seagrass (without ghost shrimp controls) and in the number of mounds between treatments that included ghost shrimp (without seagrass control plots) were statistically analysed by applying two-way crossed ANOVA, involving treatment and time (start and end of the experiment) as factors and including interactions (Zar, 1996). One-way ANOVA was applied to seagrass below-ground biomass data from each treatment at the end of the experiment (excluding ghost shrimp controls), including *post hoc* least significant difference tests (LSD Bonferroni) (Zar, 1996). Prior to significance testing, all data were graphically assessed for normality, and heterogeneity of variances was evaluated using Cochran's *C*-test ($P > 0.05$) (Underwood, 1997). No data were transformed. It was presumed that data from the arbitrarily assigned treatment sites and haphazardly placed plots conformed to the assumption of random sampling necessary for the application of ANOVA.

Non-parametric Kruskal–Wallis tests were utilised to evaluate sediment turnover data from each estuary (Zar, 1996). Tests were conducted to assess differences in the amount of sediment collected from ghost shrimp burrows and in control traps at the start and end of the experiment, and differences in ghost shrimp expulsion data over time. All univariate analyses were conducted using SPSSv6.1.

The software package PRIMER (Plymouth Routines in Multivariate Ecological Research) (Clarke and Gorley, 2001) was utilised to examine and test for multivariate differences in infauna assemblage composition between treatments at the start and end of the experiment. A ranked triangular similarity matrix was derived for each sampling occasion based on the Bray–Curtis index (Bray and Curtis, 1957) on square-root transformed infauna abundance data. Square-root transformation was chosen to down-weight the importance of highly abundant species and therefore allow for the abundance of less common species to be accounted for in the analysis (Clarke and Warwick, 2001). This relatively mild transformation was considered suitable for the present study because it was predicted that both “obvious” and “subtle” changes in the infaunal assemblage composition might take place as a result of the transplantation treatments. Non-metric multidimensional scaling (MDS) ordinations were plotted to visually assess differences in assemblage compositions between treatments (Field et al., 1982), and formal significance testing was conducted through one-way analysis of similarities (ANOSIM) (Clarke and Green, 1988). Taxa

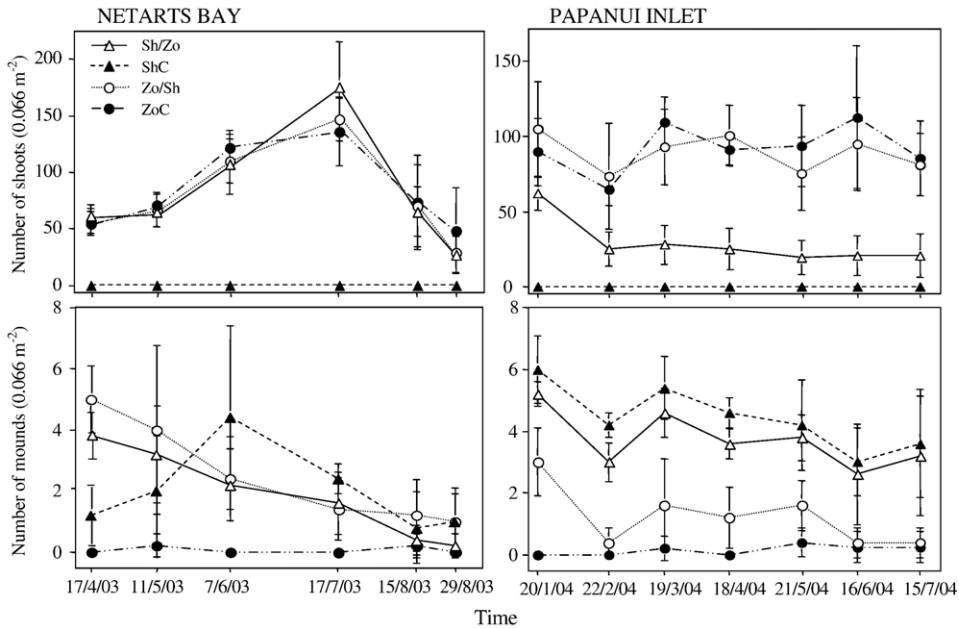


Fig. 2. Mean values for number of seagrass shoots and number of ghost shrimp mounds in each treatment in Netarts Bay and Papanui Inlet over time (ShC = ghost shrimp control, ZoC = seagrass control, Sh/Zo = ghost shrimp sites with seagrass transplants, Zo/Sh = seagrass sites with ghost shrimp transplants (vertical bars = 2SE) (Note different scales on y-axis of seagrass shoot data).

contributing to dissimilarities between pairs of treatments were ascertained using the similarity percentages procedure SIMPER (Clarke, 1993). The correlation-based BVSTEP routine (Clarke and Warwick, 2001) was utilised to assess the relationship between multivariate assemblage composition and the following measured environmental parameters: number of shoots, seagrass above-ground and below-ground biomass, seagrass debris, number of ghost shrimp mounds, sediment chlorophyll *a*, % total organic carbon, % sand (particles > 63 μm), % fines (particles < 63 μm , silt and clay). Prior to BVSTEP analysis, variables were assessed for multivariate normality using “draftsman plots” (Clarke and Ainsworth, 1993). Co-correlation of environmental variables was assessed by Spearman’s Rank Correlation (cut-off $\rho = 0.95$), and % sand (which co-correlated with % fines) was subsequently omitted from analysis.

3. Results

3.1. Interaction between ghost shrimp and seagrass

In Netarts Bay, seagrass shoot density showed similar values and fluctuations in all treatments that contained *Z. japonica*, with no significant differences over the spring–summer time period over which the experiment was conducted (Fig. 2, Table 1). The number of

artificially established seagrass shoots in ghost shrimp plots (Sh/Zo) reflected the immediate survival of all seagrass transplants at the start of the study in spring (April). Over time, shoot density in all seagrass treatments increased consistently and reached maximum densities in midsummer (July). Over the following six weeks, shoot numbers declined dramatically and few seagrass shoots were present in any of the treatments at the termination of the study at the end of the summer (late August) (Fig. 2). There was no recruitment of *Z. japonica* plants to ghost shrimp control (ShC) plots.

At the same time in the same estuary, counts of the number of *N. californiensis* mounds revealed a significant difference between treatments, over time, and between treatment and time (Table 1). All transplanted ghost shrimp succeeded in burrowing within the first 24 h of the experiment, resulting in high mound density values in seagrass sites into which ghost shrimp had been transplanted (Zo/Sh) (Fig. 2). Mound density was also high at ghost shrimp sites that included transplanted seagrass (Sh/Zo). In both ghost shrimp and seagrass transplant plots (Zo/Sh and Sh/Zo) values for the number of mounds were similar and exhibited a steady decline throughout the study period (Fig. 2). In contrast, the number of mounds in ghost shrimp control plots (ShC) was initially lower, but showed a marked increase during the first part of the study to a peak in early summer (June),

Table 1

Results from two-way crossed ANOVA (Factors: Treatment, time, and interactions) for number of shoots and number of mounds in Netarts Bay and Papanui Inlet (significant values in bold)

		Treatment		Time		Treatment × time	
		F	P	F	P	F	P
Netarts Bay	Number of shoots	0.01	0.994	1.40	0.249	0.16	0.849
	Number of mounds	9.32	0.001	40.68	0.001	7.30	0.003
Papanui Inlet	Number of shoots	13.09	0.001	6.39	0.019	1.37	0.274
	Number of mounds	13.52	0.001	20.42	0.001	0.12	0.890

before decreasing to similar values of mound density as in transplant treatments at the end of the study period (Fig. 2).

There was some recruitment of ghost shrimp to seagrass control plots (ZoC) on a couple of occasions, however, this did not appear to reflect a permanent establishment of a ghost shrimp population.

In Papanui Inlet, the number of *Z. capricorni* shoots was significantly different between treatments and over the summer–winter time period over which the experiment was conducted (Table 1). Shoot density in seagrass control treatments and at seagrass sites that contained transplanted ghost shrimp (ZoC and Zo/Sh) remained similar and at relatively high levels throughout the experiment (Fig. 2). In contrast, the number of transplanted shoots at ghost shrimp sites (Sh/Zo) exhibited considerably lower values at the start of the plot monitoring, indicating a loss of 48% of transplanted shoots immediately following transplantation. Shoot number continued to decrease in the remaining summer months of the experiment, and stayed subsequently at much lower values (approximately 20 shoots/plot) than in the other seagrass treatments. There was no recruitment of seagrass plants to ghost shrimp control (ShC) plots.

At the same time in the same estuary there was a significant difference in the number of shrimp mounds

between treatments and over time (Table 1). *Callinassa filholi* mound density was similar in ghost shrimp control treatments and ghost shrimp treatments that included transplanted seagrass (ShC and Sh/Zo), but was markedly lower at seagrass sites that contained transplanted ghost shrimp (Zo/Sh). Ghost shrimp appeared to recruit to a very low population level in seagrass control plots (Fig. 2).

At the end of the experiment in Netarts Bay, seagrass below-ground biomass varied significantly between treatments that contained *Z. japonica* ($df=2$, $F=4.28$, $P=0.039$), and ghost shrimp sites that contained seagrass transplants (Sh/Zo) exhibited the largest amount of below-ground material (Fig. 3A). At Papanui Inlet, below-ground biomass of *Z. capricorni* also exhibited significant differences between treatments at the end of the study ($df=2$; $F=6.53$, $P=0.012$). The amount of seagrass below-ground material was significantly lower in ghost shrimp treatments that contained transplanted seagrass shoots (Sh/Zo) than in seagrass treatments that contained transplanted ghost shrimp and in seagrass controls (Zo/Sh and ZoC)(Fig. 3B). Values for below-ground biomass were an order of magnitude higher in the latter two treatments than at sites that contained transplanted seagrass.

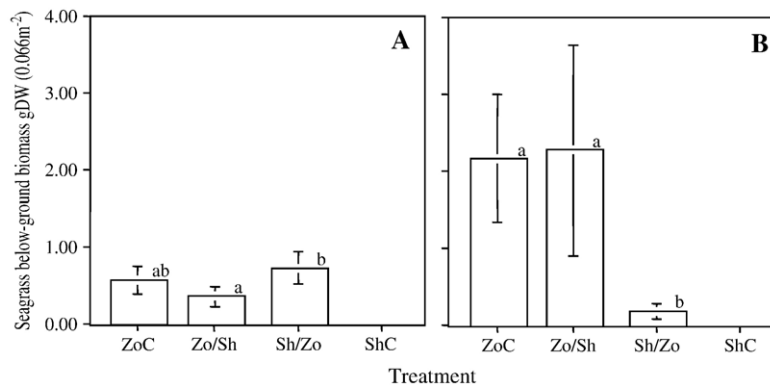


Fig. 3. Mean amount of seagrass below-ground biomass (dry weight, DW) in all seagrass treatments at the end of the transplant experiment in Netarts Bay (A) and Papanui Inlet (B) (vertical bars = 2SE). Like letters above bars (a, b, c) indicate that means are not significantly different (least significant difference test at $P<0.05$).

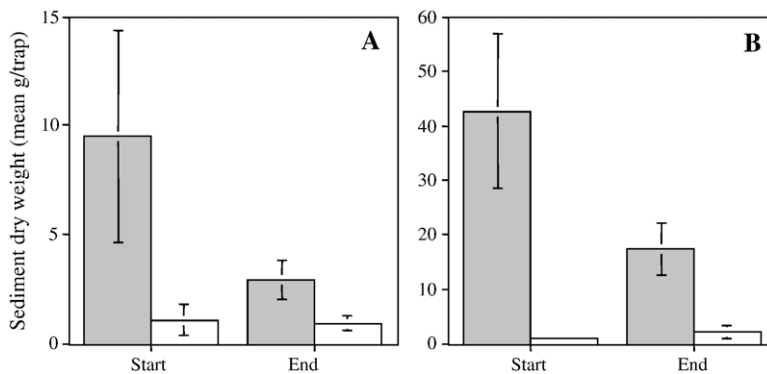


Fig. 4. Mean amount of sediment collected from ghost shrimp burrows (filled bars) and non-burrow control areas (open bars) over 24 h period at the start and end of the transplant experiment in Netarts Bay (A) and Papanui Inlet (B) (vertical bars = 2SE) (Note: different scale on y-axis).

In each estuary, the amount of sediment collected in control traps was significantly smaller than sediment collected from ghost shrimp burrows ($\chi^2=26.33$ and 27.63 for Netarts Bay start/end, $\chi^2=38.62$ and 23.06 for Papanui Inlet start/end, $P<0.001$ both estuaries, both times) (Fig. 4). Sediment turnover activity by burrowing ghost shrimps was significantly higher at the start of the transplant experiment than at the end ($\chi^2=5.24$ and 12.64 for Netarts Bay and Papanui Inlet, respectively, $P<0.05$ both estuaries). *Callianassa filholi* in Papanui Inlet exhibited notably higher bioturbation rates (approx. four times) than *N. californiensis* in Netarts Bay (Fig. 4).

4. Response of infaunal assemblages

Infauna assemblages in Netarts Bay comprised a total of 31 taxa, whereas 50 taxa were identified from treatment sites in Papanui Inlet.

As evident from the MDS ordination plots (Fig. 5), in both estuaries there was a similar pattern in the infauna assemblage compositions of the treatments at the start and end of the study. Seagrass and ghost shrimp control sites clustered separately from one another at both the start and the end of the study, indicating that the infauna assemblages of these sites were distinctly dissimilar in composition (Fig. 5). At the start of the study, seagrass controls in particular were characterised by very similar assemblage compositions, with treatment replicates clustered in close proximity to each other. At the end of the experiment, in Netarts Bay, seagrass sites that contained ghost shrimp transplants (Zo/Sh) were grouped with ghost shrimp controls (ShC), whereas ghost shrimp sites that included seagrass transplants (Sh/Zo) were mixed with seagrass controls (ZoC) (Fig. 5). In Papanui Inlet, there was a general separation between sites that initially contained seagrass (ZoC and

Zo/Sh) and those that originally included ghost shrimp (ShC and Sh/Zo) (Fig. 5).

ANOSIM permutation tests confirmed significant differences in assemblage composition between treatments at the start and end of the experiment (Table 2). In Netarts Bay, differences (Global R : 0.384 and 0.368) were significant both times, and pairwise tests revealed that at the end of the study this overall difference was due to significant differences between seagrass and ghost shrimp control sites (ZoC and ShC), ghost shrimp control sites and ghost shrimp sites that contained transplanted seagrass (ShC and Sh/Zo), and between seagrass control treatments and seagrass sites that included transplanted ghost shrimp (ZoC and Zo/Sh) (Table 2). At the same time, infauna assemblages at seagrass sites with transplanted ghost shrimp (Zo/Sh) were not significantly dissimilar to those at ghost shrimp control sites (ShC) and to those at ghost shrimp sites with transplanted seagrass (Sh/Zo), whereas the latter were not dissimilar to seagrass control sites (ZoC) (Table 2).

In Papanui Inlet, significant differences (Global R : 0.820 and 0.502) between treatments at the start and end of the experiment were more pronounced than in Netarts Bay. ANOSIM pairwise comparisons revealed significant differences in assemblage composition between seagrass and ghost shrimp controls (ZoC and ShC), and between seagrass and ghost shrimp transplant treatments (Sh/Zo and Zo/Sh). At the same time, seagrass sites with transplanted ghost shrimp (Zo/Sh) were not significantly dissimilar to seagrass controls (ZoC), but were significantly dissimilar in assemblage composition to ghost shrimp control treatments (ShC). Infauna assemblages at ghost shrimp sites with transplanted seagrass (Sh/Zo) were not dissimilar to ghost shrimp controls (ShC), but were significantly different to seagrass control sites (ZoC) (Table 2).

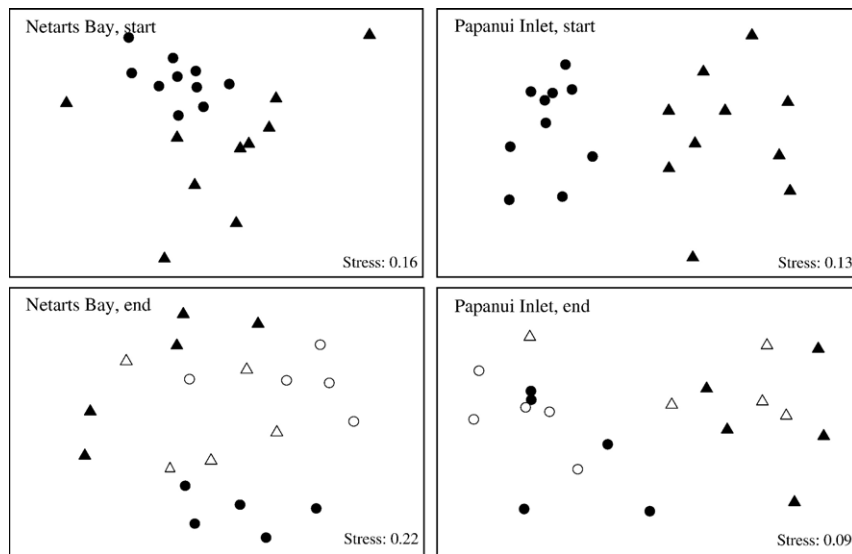


Fig. 5. MDS ordinations of infaunal abundance data ($\sqrt{\cdot}$ -transformed) from treatment locations at the start and end of transplant experiments in Netarts Bay/U.S.A. and Papanui Inlet/New Zealand (Treatments: seagrass = circles, shrimp = triangles, filled = control, open = transplant).

Similarity percentages (SIMPER) analyses of infauna abundance data for significantly different treatment groupings (data were combined where treatments were not significantly different from one another) revealed the extent of the average dissimilarity between treatments and between treatment groupings in each estuary at the start and end of the experiment, and identified those taxa that contributed most to the dissimilarity observed and/or discriminated (i.e. the ratio $\bar{\delta}_i/\text{SD}\delta_i$ of was >1.3) between the groups examined (Table 3). In Netarts Bay, six taxa contributed to 49% of the dissimilarity between control sites at the start of study, all of which showed higher abundances at seagrass than ghost shrimp control sites. The cumacean *Cumella vulgaris* contributed the most to the observed dissimilarity and, with the tanaid *Sinelobus stanfordi* and oligochaetes discriminated the best between the infaunal assemblages in seagrass and ghost shrimp control treatments. At the end of the study, dissimilarities between ghost shrimp controls plus ghost shrimp transplants (ShC and Zo/Sh) and seagrass control treatments plus seagrass transplants (ZoC and Sh/Zo) were notably smaller ($\sim 20\%$), and five taxa contributed to 50% of the dissimilarities between treatment pairs (Table 3). These taxa were the polychaetes *Streplospio benedicti*, *Pseudopolydora kempfi*, and *Capitella* sp., and the amphipod crustaceans *Corophium acherusicum* and *Grandidierella japonica*. All discriminating taxa showed higher abundances in the treatment pair that consisted of seagrass controls and seagrass transplants.

In Papanui Inlet, eight and seven taxa, respectively contributed to 56% of the dissimilarity observed

between the infauna assemblage compositions of treatments at the start and end of the study (Table 3). Of these taxa, four taxa were identified as good discriminators of the differences observed in assemblage composition at the start and end of the experiment. These taxa were three amphipod crustaceans, *Paracaliope novizealandiae*, *Protophoxus australis* and *Bathymedon neozelanicus*, and the polychaete *Exogone* sp. 1. With the exception of *B. neozelanicus*, discriminating taxa were more abundant at sites that initially contained seagrass, including those with transplanted ghost shrimp (ZoC and Zo/Sh). However, the amphipod crustacean, *P. novizealandiae* which was

Table 2

Summary of results from one-way ANOSIM for differences between treatments at the start of the experiment (Shrimp, Seagrass) and end (Sh/Zo, ShC, Zo/Sh, ZoC) of the transplant experiment in Netarts Bay and Papanui Inlet, including global and pair-wise significant levels

		ShC		ZoC		Zo/Sh	
		R	P	R	P	R	P
<i>Netarts Bay</i>							
Start	$R=0.384$, $P=0.001$						
End	$R=0.368$, $P=0.001$	ZoC	0.716	0.008			
		Zo/Sh	0.225	0.079	0.619	0.008	
		Sh/Zo	0.344	0.032	0.240	0.103	0.081
					0.280		
<i>Papanui Inlet</i>							
Start	$R=0.820$, $P=0.001$						
End	$R=0.502$, $P=0.001$	ZoC	0.840	0.008			
		Zo/Sh	0.988	0.008	0.044	0.31	
		Sh/Zo	0.000	0.460	0.468	0.024	0.640
						0.016	

Table 3

Results from SIMPER analysis, including mean abundance (α) and dissimilarity (DS) of macrofauna taxa averaged between significantly different treatments at the start and end of the experiment in Netarts Bay/U.S.A. and Papanui Inlet/New Zealand, 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)

	α_S	α_Z	$\bar{\delta}_i/$ SD δ_i	$\delta_i\%$	$\Sigma\delta_i$ %
Netarts Bay					
$(\alpha_S = \text{Shrimp}; \alpha_Z = \text{Seagrass})$					
DS = 49.23%					
<i>Cumella vulgaris</i>	13.00	49.80	2.06	17.30	17.30
<i>Capitella</i> sp.	5.50	9.10	1.29	7.63	24.92
Oligochaeta	20.70	40.30	1.51	7.58	32.50
<i>Pygospio elegans</i>	4.10	8.50	1.14	7.07	39.58
<i>Sinelobus stanfordi</i>	0.70	2.70	1.32	4.31	43.88
<i>Grandidierella japonica</i>	2.60	5.20	1.07	4.17	48.05
End					
$(\alpha_S = \text{ShC}; \alpha_Z = \text{ZoC})$					
DS = 23.83%					
<i>Streblospio benedicti</i>	3.40	28.80	2.01	13.23	13.23
<i>Capitella</i> sp.	43.40	50.40	1.27	10.09	23.32
<i>Corophium acherusicum</i>	107.00	160.20	1.69	9.19	32.50
Oligochaeta	4.40	15.80	1.89	7.78	40.28
<i>Grandidierella japonica</i>	132.00	147.40	1.41	7.29	47.56
$(\alpha_S = \text{Zo/Sh}; \alpha_Z = \text{ZoC})$					
DS = 22.21%					
<i>Capitella</i> sp.	13.00	50.40	1.60	16.00	16.00
<i>Streblospio benedicti</i>	8.50	28.80	1.73	11.70	27.70
<i>Grandidierella japonica</i>	119.25	147.40	1.32	8.12	35.82
Ostracoda	4.50	2.00	1.83	6.29	42.11
<i>Pseudopolydora kempfi</i>	18.75	11.60	1.25	6.14	48.25
$(\alpha_S = \text{ShC}; \alpha_Z = \text{Sh/Zo})$					
DS = 20.91%					
<i>Capitella</i> sp.	43.40	39.80	1.41	11.61	11.61
<i>Corophium acherusicum</i>	107.00	149.00	1.71	10.84	22.45
<i>Pseudopolydora kempfi</i>	13.60	25.40	1.29	8.72	31.17
<i>Sinelobus stanfordi</i>	0.20	4.20	2.64	8.45	39.62
<i>Ampithoe valida</i>	0.40	4.20	1.56	7.44	47.06
Papanui Inlet					
$(\alpha_S = \text{Shrimp}; \alpha_Z = \text{Seagrass})$					
DS = 55.88%					
<i>Paracalliope novizealandiae</i>	3.70	17.30	1.89	6.89	6.89
<i>Protophoxus australis</i>	0.10	9.20	1.58	6.88	13.77
<i>Exogone</i> sp. 1	0.00	8.70	1.33	6.67	20.44
Exogonidae 1	5.20	9.50	1.49	6.12	26.56
<i>Nucula hartvigiana</i>	18.70	23.00	1.38	5.35	31.91
<i>Bathymedon neozelanicus</i>	5.30	0.10	1.63	5.34	37.25
Oligochaeta	10.30	25.90	1.04	4.96	42.21
<i>Torridoharpinia hurleyi</i>	4.20	9.90	1.33	4.34	46.55
End					
$(\alpha_S = \text{Sh and ShC};$ $\alpha_Z = \text{Zo and ZoC})$					
DS = 56.07%					
<i>Protophoxus australis</i>	2.00	36.60	2.07	10.38	10.38
Oligochaeta	19.90	60.90	1.55	9.61	19.99
<i>Bathymedon neozelanicus</i>	21.50	0.40	3.20	9.04	29.03
<i>Exogone</i> sp. 1	8.60	23.90	1.58	5.93	34.96

Table 3 (continued)

	α_S	α_Z	$\bar{\delta}_i/$ SD δ_i	$\delta_i\%$	$\Sigma\delta_i$ %
DS = 56.07%					
Terebellidae	1.40	11.30	2.33	5.53	40.50
<i>Parawaldeckia</i> sp.	1.00	8.00	1.41	4.12	44.61
<i>Paracalliope novizealandiae</i>	26.50	16.80	1.43	4.03	48.64

more abundant at seagrass control sites (ZoC) at the start of the study, was relatively less abundant at the treatment grouping of seagrass controls and seagrass with ghost shrimp transplants (ZoC and Zo/Sh) at the end of the experiment.

Of the eight environmental variables included in the BVSTEP analysis, seagrass above-ground biomass best explained ($\rho_w = 0.399$) the observed infauna assemblage composition at ghost shrimp and seagrass sites in Netarts Bay, at the start of the experiment. At the end of study, the combination of the number of shoots, seagrass above-and below ground biomass and % fines produced the best overall correlation ($\rho_w = 0.305$) between environmental factors and assemblage composition in the four different treatments. In Papanui Inlet, number of shoots, seagrass above-ground biomass, and chlorophyll *a* had the highest explanatory power ($\rho_w = 0.753$) at the start of the study, whereas four variables, number of shoots, seagrass above-ground biomass, % total organic carbon and % fines, showed the best correlation ($\rho_w = 0.620$) with assemblage composition at the end of the experiment.

5. Discussion

The outcome of each transplant experiment, conducted at different times of the year, revealed different interactions between seagrass and burrowing ghost shrimp. In Netarts Bay (spring–summer), the relationship between *Z. japonica* and *N. californiensis* appeared to be uni-directional with the seagrass dominating the association. *Z. japonica* prospered in all treatments, particularly at sites where shoots had been transplanted into ghost shrimp plots, where it increased in biomass in spite of the presence of *N. californiensis*. At the same time, mound density diminished in both types of transplant treatments, indicating a general decrease in *N. californiensis* sediment turnover activity and abundance at sites where *Z. japonica* was present.

In Papanui Inlet (summer–winter), the interaction between *Z. capricorni* and *C. filholi* appeared to be reciprocal in both types of transplant treatments; the number of transplanted seagrass shoots declined whilst

mound density remained high in ghost shrimp treatments, whereas the opposite scenario was evident in seagrass plots that contained transplanted ghost shrimp. Data from this inlet indicate that the engineering species initially present at each site was unaffected by the addition of a transplanted species, whereas reciprocal transplants of either type of organism did not become dominant.

Observed differences in seagrass–shrimp interactions might be related to differences in the timing of the experiment in each of the estuaries. In Netarts Bay, the study commenced in spring, at a time of maximum seagrass growth, and it is likely that the rapid expansion of *Z. japonica* during this season was effective in reducing the number of ghost shrimp in seagrass plots. In contrast, in Papanui Inlet where the experiment was started in the middle of summer, transplants of *Z. capricorni* and *C. filholi* did not become established, and this may have been due to a peak in *Z. capricorni* biomass coinciding with high sediment turnover activity by *C. filholi*, precluding the establishment and subsequent expansion of reciprocal transplants. Logistical constraints precluded the same seasonal starting point for each transplant experiment and, therefore, the seasonal difference might explain some of the observed interaction.

The importance of seasonal timing in regards to seagrass–ghost shrimp interactions has been highlighted in a previous study, in a northern temperate estuary (Harrison, 1987). Following the artificial addition of *Z. japonica* to high-density *N. californiensis* areas in early summer, ghost shrimp abundance exhibited a marked reduction. During summer, however, *N. californiensis* populated areas from which *Z. marina* and *Z. japonica* had been removed (Harrison, 1987). Harrison (1987) speculated that the observed shifts in abundance were related to an offset in peak growth and maximum activity of seagrass and ghost shrimp, respectively. During summer, when bioturbation rates were high and an unstable substrate and high sediment resuspension possibly made the habitat unsuitable for seagrass, ghost shrimp were able to invade low density seagrass areas (Harrison, 1987). At a time of rapid growth in spring and early summer, however, an increase in biomass might have provided the seagrass with a competitive advantage in areas where ghost shrimp numbers were reduced, as dense roots and rhizomes may deter ghost shrimp from burrowing (Brenchley, 1982). Although the presence of seagrass in the present study did not prevent initial re-burrowing, dense roots and rhizomes possibly precluded the long-term establishment of transplanted ghost shrimp in seagrass plots. As burrow ventilation

and the ejection of sediment are facilitated through the upper part of ghost shrimp burrows (Stamhuis et al., 1996; Ziebis et al., 1996), any obstruction such as dense roots and rhizomes is likely to have a severe impact on burrowing functioning. Although ghost shrimp can circumvent obstacles at a particular depth and maintain their burrows (Miller and Curran, 2001), the presence of seagrass below-ground biomass in the entire top 10–15 cm of the sediment is likely to hinder essential burrowing activities.

In as much as seasonal timing might have affected the outcome of the two transplant experiments, interspecific differences between the pairings of seagrass and ghost shrimp could have also played a role. In the present study, in the Pacific Northwest, the combination of *Z. japonica*/*N. californiensis* was characterised by a rapidly expanding seagrass and a ghost shrimp species with low sediment turnover activity. The ability of *Z. japonica* to expand quickly has previously been reported by Harrison and Bigley (1982), who studied the biology of *Z. japonica* in British Columbia, Canada (Pacific Northwest). They noted that low-density seagrass patches of less than 8 shoots 0.25 m^{-2} increased more than tenfold over a short period of time (c. 4 months). Posey (1988) who studied *Z. japonica* in Coos Bay/Southern Oregon (Pacific Northwest) also noted a rapid spread of this species, and observed the establishment of seagrass patches in areas where they were initially absent over a 9-month period. Data from transplant plots in Netarts Bay confirm that individually transplanted shoots quickly became established and rapidly increased in biomass, including below-ground roots and rhizomes. It is therefore likely that the successful establishment of *Z. japonica* was related to this species' ability to quickly increase in biomass during spring and summer. Low sediment turnover activity by *N. californiensis* might have contributed to the relative success of the quickly expanding *Z. japonica*.

Even during summer, bioturbation rates of *N. californiensis* were only 25% of those reported for its southern hemisphere counterpart, *C. filholi* (this study, and see Berkenbusch and Rowden, 1999, in press). Ghost shrimp bioturbation has been implicated as one of the main physical factors impacting seagrasses in the Tropics (Roberts et al., 1981; Suchanek, 1983), and although sediment turnover rates of *C. filholi* (e.g., 47.11 ± 11.0 dry sediment mound $^{-1}$ day $^{-1}$ — Berkenbusch and Rowden, 1999) are lower than those of similar-sized tropical species of callianassid (*Callianassa* sp. 158 ± 127 dry sediment mound $^{-1}$ day $^{-1}$ — Suchanek, 1983), it is possible that bioturbation by *C. filholi* was sufficient to negatively

impact on the establishment of *Z. capricorni* in treatment plots, particularly during the summer months. In plots where seagrass was already established, however, burrowing and sediment turnover activity by ghost shrimp appeared to be insufficient to impact on *Z. capricorni* (similarly for *N. californiensis* and *Z. japonica*).

It is worth noting that the decline in *Z. japonica* density at the end of the experiment in Netarts Bay was drastic and unexpected (Fig. 2). *Z. japonica* data from another Oregon estuary (Yaquina Bay) showed a markedly slower seasonal decrease in shoot density with minimum values observed at the end of winter (Kaldy, 2006). The reason for the sudden decrease in *Z. japonica* above-ground biomass is unknown, but the sudden decline was evident across the entire seagrass area in Netarts Bay (K.B. pers obs.).

Infauna assemblage composition in both estuaries reflected the presence of the dominant type of organism, and thereby, the relative success of transplanted seagrass and ghost shrimp, respectively. In Netarts Bay, where seagrass and ghost shrimp transplants became established, infauna assemblage compositions in transplant plots were similar to the corresponding control plots of the respective transplanted organism.

Even though shoot and mound density declined over the course of the study, infaunal composition was determined by the type of organism transplanted ca. 4 months previously.

Differences in assemblage composition between seagrass and ghost shrimp plots were determined by discriminating taxa that showed higher abundances in seagrass treatments, and were generally related to variables directly linked to seagrass — number of shoots, above- and below-ground biomass, and % sediment fines (equivalent to co-correlated % sand). An earlier mensurative study, which assessed intertidal infaunal assemblage composition in relation to naturally occurring differences in seagrass and ghost shrimp density revealed distinct benthic assemblages associated with the dominant type of organism, which was consistent across different-sized estuaries in two temperate regions (Berkenbusch and Rowden, in press). Within each estuary, seagrass and ghost shrimp exerted their influence over a small spatial scale (metres), and seagrass sites were characterised by higher infauna densities than ghost shrimp sites. This prevalence of infauna appeared to be related to variables indirectly linked to seagrass — i.e., % sediment fines, % sediment carbon, and seagrass debris, possibly reflecting a greater availability of detrital and organic matter for episammic infauna in seagrass areas (Berkenbusch and Rowden, in press).

Differences in the availability of food seemed to also play a major role in the present study, as the majority of discriminating taxa were mobile or tube-dwelling deposit feeders, including oligochaetes, spionid polychaetes (*Pygospio elegans*, *S. benedicti*, *P. kempfi* — United States; *Exogone* sp. 1, Exogonidae 1 — New Zealand) and amphipod crustaceans (*G. japonica*, *C. acherusicum* — United States; *P. australis*, *Torridoharpinia hurleyi* — New Zealand), which directly benefit from a higher amount of detrital matter in seagrass plots. At the same time, the absence (or low abundance) of deposit feeding ghost shrimp in plots dominated by seagrass presumably diminishes direct competition for food between ghost shrimp and smaller infaunal species. The notion of food availability as one of the determining forces for infauna assemblage patterns in seagrass and ghost shrimp habitats was supported by the lower abundance of the amphipod *B. neozelanicus* at sites dominated by seagrass in New Zealand. As *Bathymedon* spp. purportedly feed on meiofauna (Cartes et al., 2002), *B. neozelanicus* would not directly benefit from increased seagrass biomass and sediment fines.

Enhanced food supply has been accredited for a positive association between infaunal macroinvertebrates and seagrass in a number of studies that compared seagrass beds to unvegetated areas (Posey, 1988; Castel et al., 1989; Edgar et al., 1994; Bostroem and Bonsdorff, 1997; Lee et al., 2001). Stable isotope analysis has identified *Z. marina* as an important carbon source for dominant consumers in the associated faunal community (Thayer et al., 1978; Kharlamenko et al., 2001) and the assimilation of seagrass material occurs either directly or through bacterial and microbial pathways (Penhale and Smith, 1977; Jernakoff and Nielsen, 1998; Kharlamenko et al., 2001; Lee et al., 2001; Luczkovich et al., 2002). In addition, seagrass above-ground material enhances the food supply to the benthos through its influence on the local hydrodynamic environment (Fonseca and Fisher, 1986; Gambi et al., 1990). As seagrass leaves reduce current velocities and shear stress within the canopy, the baffling of water motion results in enhanced organic deposition and the accumulation of sediment fines (Fonseca and Fisher, 1986; Gambi et al., 1990), which in turn promote associated faunal communities.

The general importance of the number of seagrass shoots and above-ground biomass has been highlighted in studies that investigated differences in canopy density and height in relation to faunal communities, but the majority of studies have focused on epi-rather than infaunal assemblages. Lee et al. (2001) used artificial seagrass transplants to mimic *Z. japonica* patches of different shoot density and leaf height. After three months, the abundance

of total epifauna and of some of the discriminating taxa was significantly higher in high-density/long-leaf treatments than in controls (no above-ground material) (Lee et al., 2001). Similarly, reduction of *Cymodocea nodosa* canopy height to one third of its natural length and the removal of the entire seagrass canopy resulted in consistent differences in faunal assemblages compared to fauna in non-manipulated plots; the abundance and biomass of total epifauna and some of its key taxa decreased with the reduction in seagrass cover within two days, and this response was similar across different faunal assemblages at two separate sites (Connolly and Butler, 1996). An examination of infaunal assemblages in relation to naturally occurring differences in *Z. marina* density also revealed significant differences in community structure between the shoot density ranges sampled, with a reduction in diversity corresponding to a decrease in shoot density (Webster et al., 1998).

The significance of the above-ground component of seagrass for associated macrofauna has been attributed to a myriad of underlying mechanisms (Lewis 1984; Orth et al., 1984; Peterson et al., 1984; Lee et al., 2001), but it is difficult to single out the most important determinant for the infaunal component of associated communities. The reduction of hydrodynamic forces by the above-ground component of the seagrass not only results in an enhanced food supply, but also stabilises the sediment (Orth, 1977) and promotes faunal settlement (Eckman, 1983; Peterson, 1986) — all of which could be beneficial to the infauna. In addition, the presence of above-ground shoots and leaves are likely to afford infauna greater protection from predators than they experience in unvegetated areas of soft-sediment, as has been suggested previously for infauna (Webster et al. 1998). Webster et al. (1998) also postulated that with differences in the above-ground structure of seagrass there are likely to be corresponding differences in the structural heterogeneity of the root–rhizome matrix, which in turn would influence the composition of the infaunal assemblage. The same authors noted that gross parameters such as below-ground biomass would alone not be particularly useful for elucidating whether or how the below-ground component of seagrass influences infaunal composition (in the present study, below-ground biomass was indicated as having explanatory power for the assemblage pattern observed at the end of the experiment in Netarts Bay).

There is then a need for future studies to determine the exact mechanisms by which the various parameters of seagrass influence the infaunal component of associated communities. Such studies will need to include laboratory/mesocosm experiments to explicate the nature and relative contribution of multiple mechanisms.

The present study reveals the capacity of sympatric seagrass and ghost shrimp species to invade adjacent areas. This finding has important implications for understanding how disturbances might affect the distributional balance of co-occurring ecosystem engineers. For seagrass and ghost shrimp, the success of the invasion appears to be dependent on the timing of the disturbance (in this case the transplantation) and the species involved. Ideally, the sort of field experiment carried out during the present study would be repeated with different (seasonal) start times and be extended to an examination of seagrass–ghost shrimp interactions in the Tropics, where formal recognition of these kinds of interactions were first recognised.

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