

Seagrass (*Zostera muelleri*) patch size and spatial location influence infaunal macroinvertebrate assemblages

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ARTICLE INFO

Article history:

Received 19 February 2008

Accepted 16 October 2008

Available online 1 November 2008

Keywords:

macrofauna
seagrass
environmental factors
grain size
New Zealand
Papanui Inlet
Otago Harbour

ABSTRACT

Seagrass landscapes are coastal environments that support diverse and abundant faunal communities. This study investigated infaunal assemblage patterns in fragmented and continuous *Zostera muelleri* habitat in southeastern New Zealand. Intertidal macroinvertebrate assemblages were examined in fragmented seagrass habitat (containing discrete patches varying in size from 1 to 200 m²) and continuous meadows (>1000 m²), in a small and a large tidal inlet. Community indices differed between seagrass habitat types and the total number of taxa was significantly lower at fragmented seagrass sites in one of the inlets. The total number of individuals and diversity were significantly different between fragmented and continuous seagrass habitat in both inlets, but diversity values showed inconsistent patterns between inlets. Multivariate analysis confirmed that different seagrass habitat types support distinct macrofaunal assemblages in each inlet and position on the shore was identified as the single most important variable explaining dissimilarities in assemblage compositions. These findings confirm the influence of seagrass habitat size on infaunal assemblages and also highlight the importance of spatial position of seagrass habitat in intertidal areas.

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1. Introduction

Seagrasses have a worldwide distribution in temperate and tropical regions (Green and Short, 2003) where they grow from midlittoral zones to subtidal depths of 40–50 m in sedimentary habitats (Den Hartog and Phillips, 2001; Green and Short, 2003). There is strong evidence that the presence of seagrass enhances biodiversity through increased habitat complexity, provision of refuge, and increased food supply (Orth, 1973; Boström and Bonsdorff, 2000; Ford et al., 2001; Jenkins et al., 2002; Boström et al., 2006a). Furthermore, faunal communities in seagrass areas have been shown to be distinctly different in comparison with those in unvegetated habitat, over relatively small spatial scales (i.e., from centimetres to tens of metres) (Boström and Bonsdorff, 1997; Connolly, 1997).

Habitat fragmentation is a landscape-scale process where a single continuous habitat breaks up into smaller fragments, or “patches” (Fahrig, 2003). Biodiversity and community composition can be affected positively or negatively through the changes in size, shape, and location of the remaining habitat patches (Fahrig, 1997). For example, the reduction of continuous habitat may contribute to

increased predation rates on patch inhabitants, decreasing diversity (Andrén, 1994; Irlandi, 1994), whereas a higher edge to interior ratio in smaller patches provides a larger edge area for the interception of new inhabitants from the surrounding area, thereby may increase diversity (Harris, 1988; Eggleston et al., 1999). Landscape-scale research on habitat fragmentation has traditionally been focused on terrestrial habitats (e.g. Andrén, 1994; Fahrig, 1997; Bender et al., 1998), however, heterogeneous marine seagrass landscapes have received recent attention (e.g. Bell et al., 2001; Boström et al., 2006a).

Seagrass landscapes can become fragmented through natural biotic and abiotic factors (Fonseca et al., 1996; Hovel and Lipcius, 2001) and through anthropogenic causes (Short and Wyllie-Echeverria, 1996). At the same time, the natural expansion of seagrass results in interspersed discrete seagrass patches of varying size and age in otherwise unvegetated sediments (Posey, 1988). As a consequence, seagrass habitats are frequently characterised by mosaics of extensive, continuous meadows interspersed with discrete patches separated by bare sediment (Robbins and Bell, 1994; Borg et al., 2005).

Recent studies have shown that fragmented seagrass habitat influences the abundance, composition and survival of fauna, in response to different landscape-scale qualities, such as configuration, size and position of seagrass patches (see reviews by Bell et al., 2001; Connolly and Hindell, 2006). For example, several small seagrass beds were inhabited by a significantly greater number of

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fish and macroinvertebrates and were more diverse than a single larger bed (McNeill and Fairweather, 1993; Healey and Hovel, 2004). Similarly, infaunal assemblage composition has been shown to differ significantly between fragmented and continuous seagrass habitat (Frost et al., 1999) and also between different-sized seagrass patches (Bowden et al., 2001). In addition, the physical setting of a seagrass patch and flow-on effects from the presence of plant structure, such as increased organic matter and decrease in sediment grain size, have consistently been found to be important for infauna through the provision of shelter and nutrition (Frost et al., 1999; van Houte-Howes et al., 2004; Boström et al., 2006b).

To understand the underlying processes that determine ecological communities, it is necessary to first observe community patterns (Underwood et al., 2000). The present study assessed infaunal assemblage patterns in relation to seagrass habitat fragmentation by investigating two different types of intertidal seagrass habitat, fragmented and continuous seagrass areas, in two tidal inlets. The main questions addressed in this study were: (1) are fragmented and continuous seagrass habitat types characterised by distinctly different infaunal assemblages; and (2) are infaunal assemblage patterns associated with fragmented and continuous seagrass habitat consistent between different locations?

2. Materials and methods

2.1. Study sites and field sampling

The present study was conducted in southeastern New Zealand, in Papanui Inlet (4.1 km²) and at Harwood in Otago Harbour (46 km²) (Fig. 1). Both inlets had a similar mean tidal range, between 1 and 2 m (Heiss et al., 2000; Albrecht and Vennell, 2007) and contained large areas vegetated by seagrass, *Zostera muelleri* (previously *Zostera capricorni*) (Jacobs et al., 2006). *Zostera muelleri* is a small (blade lengths ~5–15 cm) and predominantly intertidal seagrass that occurs throughout New Zealand and in southern Australia (Inglis, 2003; Turner and Schwarz, 2006). In New Zealand, *Z. muelleri* habitat varies in extent and biomass and frequently occurs as a mosaic of different-sized patches, with extensive areas of continuous seagrass coverage being less common (Turner et al., 1999; Inglis, 2003; Turner, 2007).

Based on naturally occurring *Z. muelleri* at each location, an area of continuous seagrass (>1000 m²) and a similar sized area of fragmented seagrass (containing discrete circular seagrass patches) were selected as natural “treatment” sites. The selection of seagrass areas at each location was dictated by the presence of an extensive, continuous seagrass meadow in the same area as fragmented seagrass habitat. At Harwood, the continuous seagrass habitat was at the same tidal height as the fragmented seagrass habitat, in the low intertidal zone. In Papanui Inlet, however, extensive, continuous seagrass habitat was only located in the lower intertidal, whereas fragmented seagrass habitat was in the upper intertidal zone. This difference in spatial arrangement between fragmented and continuous seagrass areas in Papanui Inlet enabled assessment of the relative importance of spatial position within the inlet in addition to seagrass habitat type.

Five replicate samples were taken from within the continuous seagrass habitat and 10 samples were collected from within the fragmented seagrass habitat in summer and winter (Papanui Inlet, 10 February 2005 and 1 August 2005; Harwood, 9 February 2005 and 23 July 2005). Approximately circular seagrass patches (five small (1–5 m²) and five large patches (100–200 m²)) were haphazardly selected within the fragmented seagrass habitat. To avoid possible edge effects, samples were taken from the centre of each patch and 100 m from the edge in continuous seagrass habitat. The spatial position of each sample was determined by GPS. On each sampling occasion, a flat ring (10 cm Ø) was placed on the sediment. All seagrass blades within the ring were cut off at the sediment surface and retained. Macrofauna was subsequently sampled in the same position with a benthic core (10 cm Ø, 10 cm depth). An additional core (5 cm Ø, 10 cm depth) was taken adjacent to the macrofauna core for sediment grain size and organic content analysis. Sediment samples were kept frozen until analysis.

2.2. Laboratory analysis

Faunal cores were sieved on 500-µm mesh with sea water, separated from seagrass belowground material (roots and rhizomes), preserved in 50% isopropyl alcohol and stained with Rose Bengal. Macrofauna was counted and identified to the lowest practical taxonomic level, which in most cases was species.

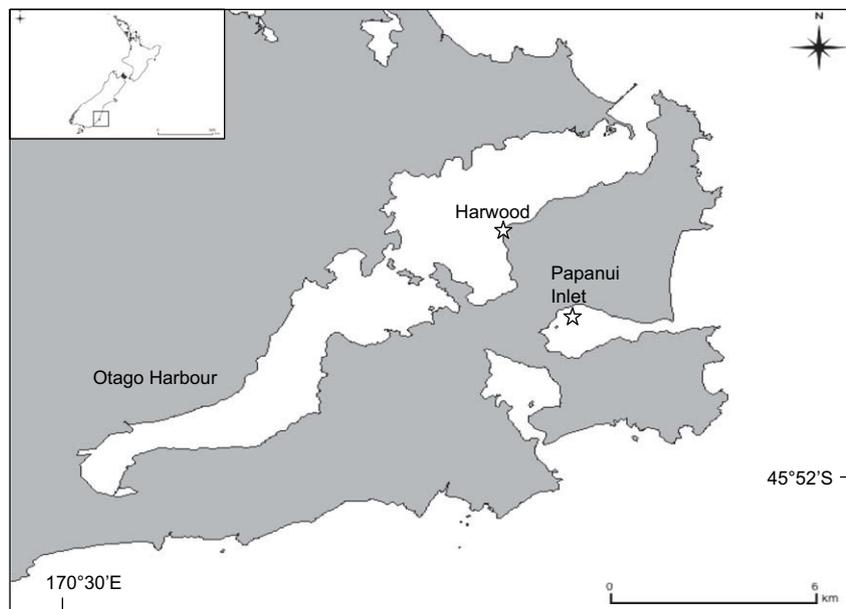


Fig. 1. Map of New Zealand indicating the location of study sites in Papanui Inlet and Harwood, Otago Harbour.

Seagrass blades and belowground seagrass material were rinsed with fresh water and any fauna attached to leaves or the rhizome mat was separated for identification. Blades and shoots were counted before above- and belowground material was dried to constant weight (60°C for 48 h). A combination of wet and dry sieving of a 100 g wet weight sediment subsample was used for sediment granulometry. Following wet sieving, the <63 µm fraction was analysed for percentage fines using pipette analysis (Lewis and McConchie, 1994). Sediment >63 µm was dried to constant weight (60°C for 48 h) and sieved at 1 phi intervals from 1 mm to 63 µm (Buchanan and Kain, 1971). An approximate 5 g subsample of sediment was combusted at 500°C for 4 h, after treatment with HCl solution (5%) to determine the percentage total organic carbon (TOC) by mass loss on ignition (Buchanan and Kain, 1971).

2.3. Data analysis

To provide a balanced data set for each inlet, five of the 10 samples from fragmented seagrass habitat were randomly selected for inclusion in subsequent univariate and multivariate analyses. Summer and winter data were combined to assess general infaunal assemblage patterns. Macrofaunal data from each inlet were analysed using the PRIMER (Plymouth Routines in Multivariate Ecological Research) software package (Clarke and Gorley, 2006). Community indices including total number of taxa, total number of individuals, and Shannon–Wiener diversity, were calculated using the DIVERSE function (Clarke and Warwick, 2001). Differences in univariate measures between continuous and fragmented seagrass habitats were tested using *t*-tests (Quinn and Keough, 2002) with a significance level of $\alpha = 0.017$ after Bonferroni adjustment for multiple tests. When necessary, data were $\log_{10}(x + 1)$ -transformed to meet assumptions of normality and homogeneity (Quinn and Keough, 2002).

Multivariate statistical methods are useful in ecological studies to analyse patterns in multiple communities of species and environmental variables and are also the most sensitive (Warwick et al., 1990; Clarke and Warwick, 2001). Macrofauna abundance data were square-root ($\sqrt{}$) transformed and a ranked similarity matrix was calculated to allow less numerically dominant species to contribute to the similarity of samples (Clarke and Warwick, 2001). Non-metric multidimensional scaling (MDS) ordinations were used to visually assess differences in macrofauna assemblages between seagrass habitat types in each inlet. Differences were formally tested with a one-way analysis of similarity (ANOSIM) (Clarke, 1993). One-way similarity percentages procedure (SIMPER) was applied to identify which taxa were responsible for any dissimilarity between samples (Clarke and Warwick, 2001; Clarke and Gorley, 2006). The relationship between macrofauna assemblage patterns and measured environmental variables was analysed with the BVSTEP routine (Clarke and Warwick, 2001). Environmental variables included in the analysis were number of leaves, number of shoots, seagrass above- and belowground biomass, % TOC, % fines, mean sediment grain size, and latitude (as a proxy for shore height/position on the shore). Prior to analysis, variables were assessed for multivariate normality using “draftsman plots” and tested for co-correlation using the Spearman rank correlation method (cut off $\rho = 0.95$) (Clarke and Warwick, 2001). As there were no co-correlates, all environmental variables were included in the BIOENV procedure. The significance level for multivariate analyses was $p < 0.05$.

3. Results

Macrofaunal assemblages in each inlet were characterised by a similar number of taxa, with 48 and 52 taxa identified in Papanui Inlet and at Harwood, respectively. In Papanui Inlet, there were

significantly less taxa in fragmented than in continuous seagrass habitat, whereas at Harwood, there was no significant difference in total number of taxa between seagrass habitats (Fig. 2, Table 1). In both inlets, total number of individuals was similarly low at fragmented seagrass sites and was significantly different to continuous seagrass habitat, which supported markedly higher infaunal densities; this difference was particularly pronounced at Harwood. Diversity also differed significantly between seagrass habitat types, but showed reverse patterns between both inlets; in Papanui Inlet, diversity was higher in continuous than fragmented seagrass habitat, whereas the opposite pattern was evident at Harwood (Fig. 2, Table 1).

Multivariate analysis revealed a clear distinction between infaunal assemblages associated with fragmented and continuous seagrass habitat in each inlet (Fig. 3). Furthermore, in Papanui Inlet, infaunal assemblage compositions in continuous seagrass habitat

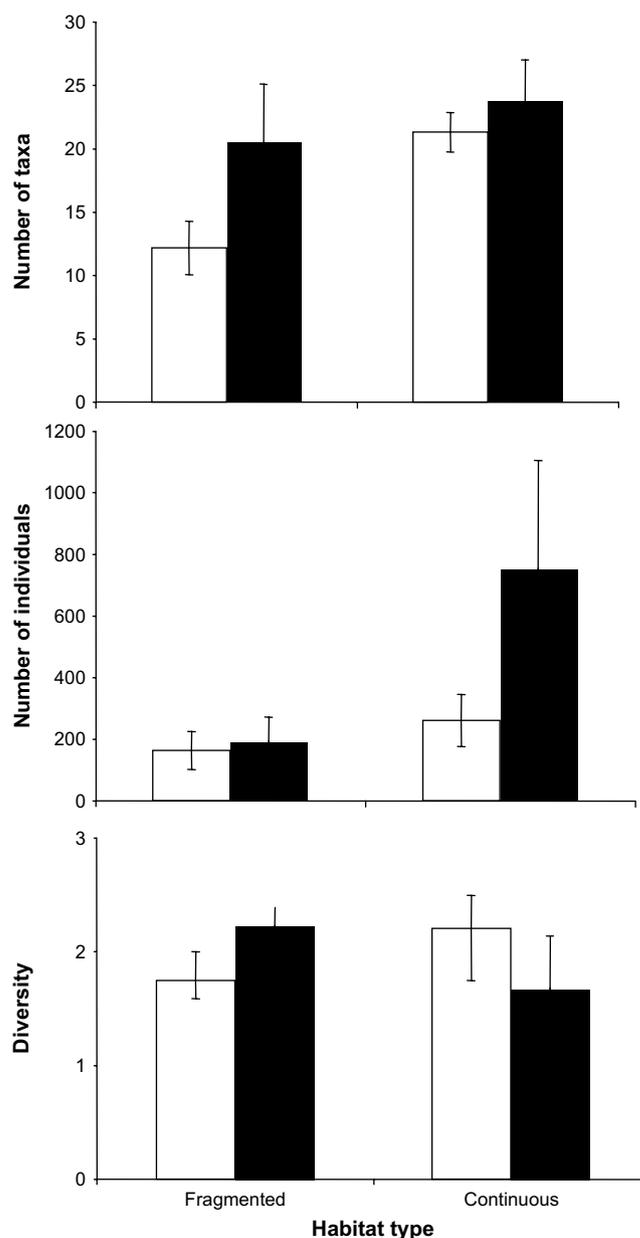


Fig. 2. Total number of taxa, total number of individuals and Shannon–Wiener diversity (mean values \pm SD per core (78.5 cm²), $n = 10$), in relation to seagrass habitat types in Papanui Inlet (open bars) and at Harwood (closed bars), southeastern New Zealand. Data for summer and winter were combined.

Table 1

Results of unpaired *t*-tests of community indices of macrofauna in fragmented and continuous seagrass habitats, including total number of taxa (*S*), total number of individuals (*N*) and Shannon–Wiener diversity (*H'*), at Papanui Inlet and Harwood, New Zealand. Significant values are highlighted in bold ($\alpha = 0.017$ following Bonferroni adjustment).

Indices	Papanui Inlet			Harwood		
	df	<i>t</i>	<i>p</i>	df	<i>t</i>	<i>p</i>
<i>S</i>	18	−10.99	<0.001	18	1.79	0.091
<i>N</i>	18	−3.08	0.006	18	4.89	<0.001
<i>H'</i>	18	−4.87	<0.001	18	−3.21	0.005

displayed relatively little variation, whereas at Harwood, assemblage compositions at fragmented seagrass sites displayed less variation than those at continuous habitat sites (Fig. 3). One-way ANOSIM confirmed the visual interpretation of the MDS ordinations and revealed significant differences in infaunal assemblages between fragmented and continuous seagrass habitat in Papanui Inlet (Global $R = 0.997$, $p = 0.001$) and at Harwood (Global $R = 0.789$, $p = 0.001$).

SIMPER analysis revealed high dissimilarities between seagrass habitat types in Papanui Inlet (73.28%) and at Harwood (59.86%). In Papanui Inlet, seven from a total of 48 taxa contributed to 50% of the dissimilarity in assemblage composition between fragmented and continuous seagrass habitat (Table 2). Five taxa, including oligochaetes, a tanaid crustacean (*Leptocheilia savignyi*), two amphipod species (*Parawaldeckia* sp. and Phoxocephalidae sp. 2), and a polychaete worm (*Aquilaspio aucklandica*), were more abundant in continuous seagrass habitat, whereas a corophiid amphipod (*Paracorophium excavatum*), and a small bivalve (*Arthritica bifurca*) were more abundant at fragmented seagrass sites. At Harwood, five out of a total of 52 taxa contributed the most (50%) to the dissimilarity between seagrass habitat types and included a small bivalve (*Perrierina turneri*), a polychaete (Syllidae sp. 2), *L. savignyi*, Phoxocephalidae sp. 2, and oligochaetes (Table 2). Except for the latter, all taxa showed markedly higher densities at fragmented than at continuous seagrass sites; for *L. savignyi* and Phoxocephalidae sp. 2 this preference was opposite to that exhibited in Papanui Inlet (Table 2).

Of the measured environmental variables, latitude, the proxy for position on the shore best explained macrofaunal assemblage patterns in Papanui Inlet (BIOENV, $\rho_w = 0.840$, $p = 0.001$). The combination of latitude and mean sediment grain size achieved the second highest correlation ($\rho_w = 0.708$) and the latter variable showed lower values at fragmented than at continuous seagrass sites (Table 3). At Harwood, latitude was the environmental variable that alone best explained assemblage patterns ($\rho_w = 0.687$), but the combination of above- and belowground seagrass biomass and TOC showed the highest correlation with macrofauna data ($\rho_w = 0.689$, $p = 0.001$). Both seagrass parameters were higher at continuous seagrass sites, whereas TOC was higher at fragmented sites (Table 3).

4. Discussion

Univariate analysis revealed mixed patterns in community variables in relation to seagrass habitat type. There was a significant difference between fragmented and continuous seagrass habitat in total number of taxa in Papanui Inlet, and macrofaunal abundances differed significantly and consistently between habitat types in both inlets, with continuous seagrass habitat supporting higher densities than fragmented sites. Species diversity also differed significantly between seagrass habitat types, but patterns between inlets were inconsistent, with lower diversity values recorded at fragmented seagrass sites in Papanui Inlet, but at continuous

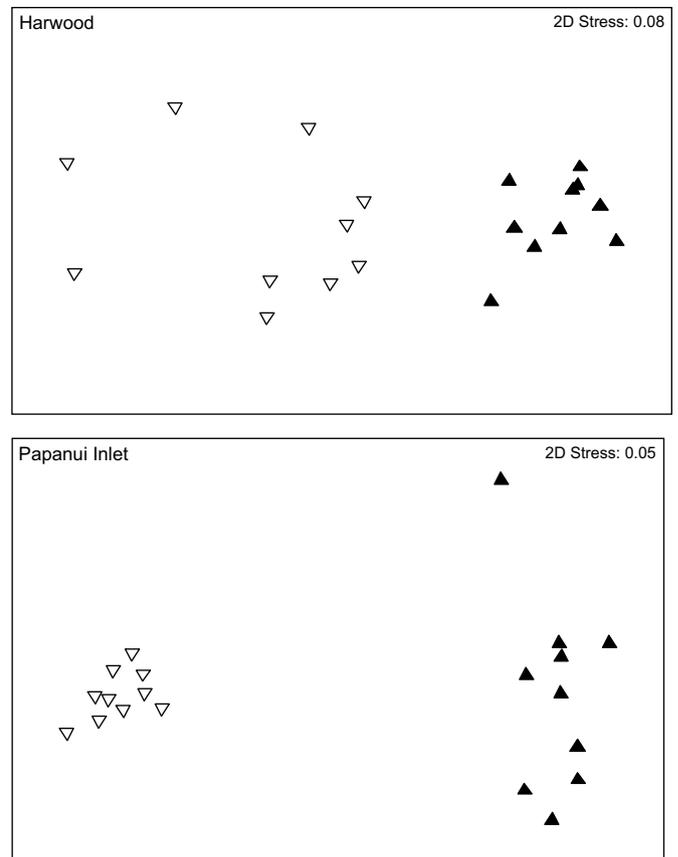


Fig. 3. Multidimensional scaling ordinations of macrofauna abundance data (square-root transformed) of fragmented (closed triangles) and continuous (open triangles) seagrass habitat in Papanui Inlet and at Harwood, southeastern New Zealand.

seagrass sites at Harwood. At the same time, multivariate analysis revealed distinct differences in macrofaunal assemblage patterns between seagrass habitat types in both inlets, owing to differences in relative abundances of common taxa.

Previous studies of infaunal assemblages in relation to fragmented seagrass habitat are limited and findings regarding univariate community indices vary, but multivariate analyses reveal consistent differences in assemblage patterns in relation to

Table 2

One-way SIMPER analysis of macrofauna data from fragmented (α_{Fragment}) and continuous ($\alpha_{\text{Continuous}}$) seagrass habitat at Papanui Inlet and Harwood, New Zealand. DS = average dissimilarity, α = mean abundance, $\delta i / \text{SD}_{\delta i}$ = ratio of contribution to dissimilarity (taxa with a ratio > 1.3 are highlighted in bold), $\delta i\%$ = percentage contribution, $\Sigma \delta i\%$ = cumulative percentage contribution (cut-off to taxa list applied at 50% cumulative contribution to dissimilarity).

DS = 73.28%	Papanui Inlet				
	α_{Fragment}	$\alpha_{\text{Continuous}}$	$\delta i / \text{SD}_{\delta i}$	$\delta i\%$	$\Sigma \delta i\%$
Oligochaeta	2.8	85.3	3.91	11.52	11.52
Paracorophium excavatum	51.0	0.6	1.84	8.82	20.34
Leptocheilia savignyi	0.0	28.5	3.64	7.33	27.67
Arthritica bifurca	16.9	0.0	2.58	5.71	33.38
Parawaldeckia sp.	0.3	16.7	2.51	5.08	38.46
Phoxocephalidae sp. 2	2.8	23.0	2.07	4.99	43.45
Aquilaspio aucklandica	0.3	11.4	3.78	4.45	47.90
DS = 59.86%	Harwood				
	α_{Fragment}	$\alpha_{\text{Continuous}}$	$\delta i / \text{SD}_{\delta i}$	$\delta i\%$	$\Sigma \delta i\%$
Perrierina turneri	369.9	18.6	2.09	17.09	17.09
Leptocheilia savignyi	247.0	16.6	2.14	14.64	31.73
Phoxocephalidae sp. 2	26.9	0.2	3.64	6.07	37.80
Syllidae sp. 2	38.5	4.4	1.79	5.15	42.95
Oligochaeta	39.9	48.1	1.28	4.14	47.09

Table 3

Mean values (\pm SD) of seagrass parameters per core (78 cm²) and sediment properties per core (20 cm²) from each seagrass habitat type ($n = 10$, combined for summer and winter) at Papanui Inlet and Harwood, New Zealand. (TOC, total organic carbon.)

Site	Habitat type	No. of seagrass leaves	Seagrass aboveground biomass (g)	No. of seagrass shoots	Seagrass belowground biomass (g)	Sediment grain size (Mean mm)	Sediment fines TOC (%)	
Papanui	Fragmented	281 (136)	1.067 (0.612)	68 (23)	4.230 (1.448)	0.126 (0.008)	3.412 (3.674)	1.585 (0.565)
	Continuous	179 (75)	0.634 (0.192)	71 (23)	5.635 (2.272)	0.147 (0.001)	2.775 (2.931)	1.789 (0.502)
Harwood	Fragmented	92 (59)	0.280 (0.135)	33 (15)	1.545 (0.740)	0.170 (0.012)	0.208 (0.137)	1.287 (0.339)
	Continuous	253 (135)	0.535 (0.264)	86 (34)	6.744 (2.607)	0.159 (0.039)	0.019 (0.059)	0.818 (0.613)

seagrass habitat size (Frost et al., 1999; Bowden et al., 2001). A study of intertidal macroinvertebrates associated with *Zostera marina* in a United Kingdom estuary revealed similar univariate community measures between seagrass patches (6–9 m²) and a continuous meadow (23,000 m²), but significant differences in overall assemblage composition (Frost et al., 1999). At three different locations at the Isles of Scilly/United Kingdom, subtidal infaunal assemblages associated with *Z. marina* patches supported a significantly higher number of taxa in large (>30 m shortest dimension) than small (<15 m longest dimension) patches, but showed no differences in abundance or diversity (Bowden et al., 2001). At the same time, multivariate analysis revealed significant patch size differences in assemblage composition, influenced by differences in the relative abundance of a number of macroinvertebrate taxa (Bowden et al., 2001). Although patch size varied between studies, these findings indicate that infaunal assemblage compositions are influenced by the relative size of seagrass habitat in intertidal and subtidal environments, with fragmented seagrass habitat supporting distinctly different assemblage compositions compared with larger, continuous beds. In the present study, patch sizes in fragmented seagrass habitat ranged between 1 and 200 m², but despite this wide range in size, univariate and multivariate faunal data from fragmented seagrass habitat showed relatively little variation. In view of these findings, it seems likely that there is a “threshold” patch size, above which infaunal assemblages in fragmented seagrass habitat are similar to those in unfragmented seagrass beds; furthermore, the threshold size appears to vary depending on the ecosystem (i.e., intertidal/subtidal) and the seagrass species involved as indicated by size differences of fragmented and continuous seagrass areas across studies.

In the present study, the position of seagrass habitat played an important role in determining infaunal assemblage patterns between seagrass habitat size. Position on the shore showed the highest correlation with macrofaunal assemblages in Papanui Inlet (and combined with mean sediment grain size ranked second highest) and was also the single variable with the highest correlation at Harwood. Position of seagrass habitat has previously been suggested to be a significant cause of variation in biodiversity (fish and decapod crustaceans) of seagrass patches in fragmented landscapes, with the location of a seagrass bed being important for enhanced larval recruitment, independent of patch size or habitat complexity (Bell et al., 1988). Bell and Hicks (1991) similarly reported that differences in meiofaunal copepod recruitment rates were due to the arrangement of the borders of seagrass vegetation in relation to the location of new recruits.

Previous macroinvertebrate studies have also highlighted the importance of the position of seagrass habitats in regards to infaunal assemblage patterns (Turner et al., 1999; Bowden et al., 2001; van Houte-Howes et al., 2004; Boström et al., 2006b). In their large-scale study of environmental factors across different *Z. marina* beds in the Baltic Sea/Finland, Boström et al. (2006b) identified sediment grain size (% fine gravel) as one of the explanatory variables for infaunal assemblage patterns; it was positively correlated with fetch sum, a measure of wave exposure, indicating the importance of hydrodynamics and of the position of

seagrass beds in determining sediment properties. At the same time, patch location, in association with fetch and shore angle, best explained macrofaunal functional group patterns (Boström et al., 2006b). In New Zealand, an assessment of infauna in *Z. muelleri* beds across different estuaries revealed marked within-estuary variability evident in significantly different macroinvertebrate community patterns between upper and lower estuary sites (van Houte-Howes et al., 2004). Similarly, spatial patterning of seagrass habitat (fractal geometry, patch isolation) at the landscape-scale appeared to affect the composition of benthic assemblages associated with *Z. muelleri* beds in two New Zealand estuaries (Turner et al., 1999).

On a smaller spatial scale, patch location had a marked influence on assemblage composition and exceeded that of patch size or within-patch location in subtidal *Z. marina* habitat (Bowden et al., 2001). The regional positioning of seagrass patches revealed the most discernible differences in infaunal assemblage parameters, which appeared to be related to differences in sediment properties (sorting, mean grain size, % fines) caused by variation in wave exposure and tidal currents (Bowden et al., 2001). In another infaunal study of fragmented and continuous *Z. marina* habitat, sediment grain size was also identified as an important variable, with the latter seagrass area containing significantly smaller sediment grain sizes than the fragmented bed (Frost et al., 1999). As different seagrass habitat types in the latter study were separated by a tidal channel, it is possible that the different location of fragmented and continuous seagrass habitat contributed to observed assemblage differences, although location was not included in the analysis of environmental factors.

In the absence of mechanistic studies, it is difficult to identify the exact causes for differences between fragmented and continuous seagrass habitats. Bowden et al. (2001) suggested that their findings supported the presence of a species-area relationship, where differences between small and large seagrass patches could be caused by different immigration and extinction rates within individual patches. As the greater proportion of fines is indicative of reduced physical disturbance (wave energy and water movement) in large patches, decreased physical disturbance would result in lower infaunal extinction rates; at the same time, immigration in the form of dispersive larvae would be greater in large seagrass areas (Bowden et al., 2001). Findings from the present study partially support this suggestion, as continuous seagrass habitats were characterised by higher numbers of individuals in both inlets, indicating higher immigration and/or lower extinction rates. Sediment grain size appeared to reflect differences in physical disturbance between seagrass habitats, but this difference was not uniformly linked to seagrass habitat size; fragmented sites in Papanui Inlet were characterised by a relatively higher % fines and lower mean grain size than continuous sites. This finding appears to be in contrast to previous studies that found smaller sized sediments characteristic of relatively larger seagrass areas (Frost et al., 1999; Bowden et al., 2001), but fragmented sites in Papanui Inlet were situated high in the intertidal and would therefore have been exposed to less physical disturbance (via tidal currents and wave actions) than the continuous seagrass habitat in this inlet.

It was unexpected that sediment properties played a relatively minor role in determining macrofaunal assemblage patterns, as previous benthic studies highlight the importance of sediment properties and document distinct infaunal assemblage patterns in relation to grain size in intertidal habitats, including unvegetated (sandflat, Giménez et al., 2006) and seagrass areas (Berkenbusch and Rowden, 2007). In addition, recent broad scale and modelling studies have confirmed the significance of sediment grain size for macrobenthic species (Thrush et al., 2003; Ellis et al., 2006). Instead of sediment grain size, seagrass above- and belowground biomass and TOC explained differences in assemblage compositions at Harwood. Webster et al. (1998) similarly found that seagrass aboveground parameters (leaf and shoot densities) were important in influencing infaunal assemblage structure across *Z. marina* beds that varied in shoot densities, whereas sediment characteristics (median grain size, silt fraction, sorting coefficient) were not. They suggested that differences in the number of leaves and shoots indirectly influenced associated infauna by influencing detrital deposition and predator efficiency (Webster et al., 1998). Detrital deposition resulting in increased sediment % fines and % carbon (linked to an increase in food for infauna) in seagrass areas was also implicated as the underlying factor determining infaunal assemblages across three southeastern New Zealand inlets, including Otago Harbour and Papanui Inlet (Berkenbusch and Rowden, 2007). At the same time, comparisons of vegetated and unvegetated areas have linked the importance of seagrass above- and belowground material to epi- and infauna to a reduction in predator efficiency and impediment of movement (Brenchley, 1982; see review by Orth et al., 1984); differences in above- and belowground biomass between fragmented and continuous sites at Harwood appeared to have been sufficiently large to influence infaunal assemblage patterns.

In agreement with previous studies (Frost et al., 1999; Bowden et al., 2001), dissimilarities between fragmented and continuous seagrass habitats were owing to changes in relative abundances of several common taxa. Taxa contributing the most to dissimilarities were benthic deposit-feeders, including amphipods (Phoxocephalidae sp. 2, *P. excavatum*, *Parawaldeckia* sp.), polychaetes (Syllidae sp. 2, *A. aucklandica*) and bivalves (*Perrierina turneri*, *A. bifurca*). Prevalence for fragmented and continuous seagrass habitat varied with taxon, and two (of three) shared taxa, the tanaid *L. savignyi* and the amphipod Phoxocephalidae sp. 2, showed opposite abundance patterns associated with seagrass habitat type between inlets. Although both taxa preferred continuous seagrass habitat in Papanui Inlet, they showed markedly (>order of magnitude) higher abundances at fragmented sites at Harwood. Considering the importance of position on the shore, this contrast could be related to avoidance of upper intertidal areas in Papanui Inlet to reduce environmental stress associated with shorter immersion times.

In conclusion, fragmented and continuous *Z. muelleri* habitats supported distinctly different infaunal assemblages in both inlets, and differences in infaunal assemblage patterns were related to the within-inlet position of seagrass habitat type. This study highlights the need for future studies to elucidate the underlying mechanisms responsible for assemblage differences between seagrass habitat types. Such assessment should include experimental field experiments that are aimed at decoupling the effect of seagrass habitat size, position and seagrass properties.

Acknowledgements

We thank Keith Probert, Kim Capone, Matthew Enright, Laurence Mills, Tessa Mills, Victor Mills and the staff at the Portobello Marine Laboratory. Many thanks to David Bowden and Ashley Rowden for statistical advice. This study was supported by a Postgraduate Award from the University of Otago to VS Mills.

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