Temporal and spatial variation in macrofauna community composition imposed by ghost shrimp *Callianassa filholi* bioturbation

Katrin Berkenbusch[1,*], Ashley A. Rowden[2], P. Keith Probert[1]

[1]Department of Marine Science, University of Otago, PO Box 56, Dunedin, New Zealand
[2]Benthic Ecology Research Group, Department of Biological Sciences, University of Plymouth, Drake Circus, Plymouth, Devon PL 8AA, United Kingdom

ABSTRACT: The impact of bioturbation by the burrowing ghost shrimp *Callianassa filholi* on benthic community composition was examined in relation to seasonal and small-scale spatial changes. Sites of naturally occurring low and high densities of *C. filholi* on an intertidal sandflat represented differences in bioturbation activity throughout the year. Univariate and multivariate analyses showed significant differences in community composition between high- and low-density sites. The total number of species and total number of individuals were lower at high-density sites. A corophiid amphipod, *Paracorophium excavatum* and a small bivalve, *Perrierina turneri*, appeared to have the greatest discriminating significance with lower abundances of both species at sites of high *C. filholi* density. Even though differences between sites of different density persisted throughout the year, the impact of bioturbation depended on season. Bioturbation had the highest maximum correlation to changes in macrofaunal community composition in winter, spring and, in association with seagrass biomass (*Zostera novazelandica*), in autumn. During summer, however, seagrass biomass contributed the most to observed differences and appeared to compensate for generally high bioturbation activity. The results imply that bioturbation impacted on macrofauna community composition over a small spatial scale and, although its impact varied seasonally, imposed patterns persisted throughout the year. As such, *C. filholi* can be considered a keystone species.

KEY WORDS: Macrofauna community · Bioturbation · *Callianassa* · Intertidal sandflat · Small scale

INTRODUCTION

Benthic community structure of soft sediment environments in tropical and temperate regions can be greatly affected by bioturbation (e.g. Myers 1977, Murphy & Kremer 1992). Feeding and burrowing activities by a variety of bioturbators (e.g. fish, hemichordates, polychaetes, holothurians, crustaceans) can cause substantial sediment disturbance in intertidal and subtidal habitats (e.g. Rhoads & Young 1971, Grant 1983). Resulting biological implications include both negative and positive effects for the abundance of associated organisms (Peterson 1977, Suchanek 1983, DeWitt & Levinton 1985, Townsend & Fonseca 1998). Suscepti-

bility to sediment disturbance varies among infaunal species, most likely related to feeding mode, size and motility of the organisms concerned, and is reflected in the overall benthic community composition (Brenchley 1981, Wilson 1981).

Despite the importance of bioturbation, few studies have examined the relationship between both temporal and spatial variations in such biological disturbance and benthic community composition (e.g. Posey 1986). Although it has been shown that rates of sediment turnover (as a measure of bioturbation) differ significantly over time (Retraubun et al. 1996), little information is available concerning this often seasonal variation and the changes it imposes on benthic community structure. Furthermore, densities of bioturbators often vary on a small scale (over 10s of metres)

*E-mail: katrin.berkenbusch@stonebow.otago.ac.nz

within one location (Swinbanks & Murray 1981), which is likely to influence the occurrence of associated fauna.

Due to their often high population densities and relatively deep burrows, callianassid shrimps (also referred to as ghost or mud shrimps) have been identified as important infaunal bioturbators with potentially the greatest effects over the largest depth range (Abu-Hilal et al. 1988, Swift 1993). Callianassid burrows are associated with unconsolidated mounds on the sediment surface, which are sources of mobile sediment in stable bottom areas, thus promoting sediment instability (Aller & Dodge 1974, Roberts et al. 1982). Furthermore, the sediment turnover activity of temperate species has been shown to differ significantly over time (Stamhuis et al. 1997, Rowden et al. 1998, Berkenbusch & Rowden 1999). However, most studies to date have examined the impact of callianassid shrimp bioturbation under laboratory conditions and/or involved experimental exclusion of ghost shrimp (by defaunation or cages, e.g. Bird 1982, Tamaki 1988, Dittmann 1996), thus potentially introducing experimental artefacts. By contrast, the present study adopted a so-called 'natural experimental' approach to examine the macrofaunal community composition in relation to temporal and spatial variations in bioturbation by the burrowing ghost shrimp *Callianassa filholi*. The aims of the study were to determine the macrofauna community composition in relation to (1) natural differences in the density of *C. filholi*, i.e. bioturbation on a relatively small but ecologically meaningful spatial scale, and (2) sea-

sonal changes in sediment turnover activity, i.e. at a pronounced temporal scale ascertained by a previous study (Berkenbusch & Rowden 1999).

Note: The systematic status of *Callianassa filholi* Milne-Edwards, 1878 is currently under review.

MATERIALS AND METHODS

Sample collection and analysis. The study site was on an intertidal sandflat in Otago Harbour, south-eastern New Zealand (45° 30' S, 170° 42' E) (Fig. 1A). Prior to sampling, 4 sites (4 × 4 m) were arbitrarily chosen to each represent low and high *Callianassa filholi* densities.

Initial selection of density groupings was based on an average of 2.5 sediment expulsion mounds m^{-2} for low density sites, and an average of at least twice as many for high density sites. Pairs of sites of the different density groupings were located on the sandflat throughout the tidal range of the shrimp's occurrence (Fig. 1B) (Berkenbusch & Rowden 1998 1999). The position of sites on the sandflat was established by triangulation in order to allow for subsequent relocation. Sampling was conducted after a period of calm weather (at least 1 wk) to minimise obliteration of mounds by wind and wave action. Samples were collected on 4 occasions—November 1997, January, April, June 1998, representing the seasons of spring, summer, autumn and winter respectively. Spring and summer have previously been identified as times of
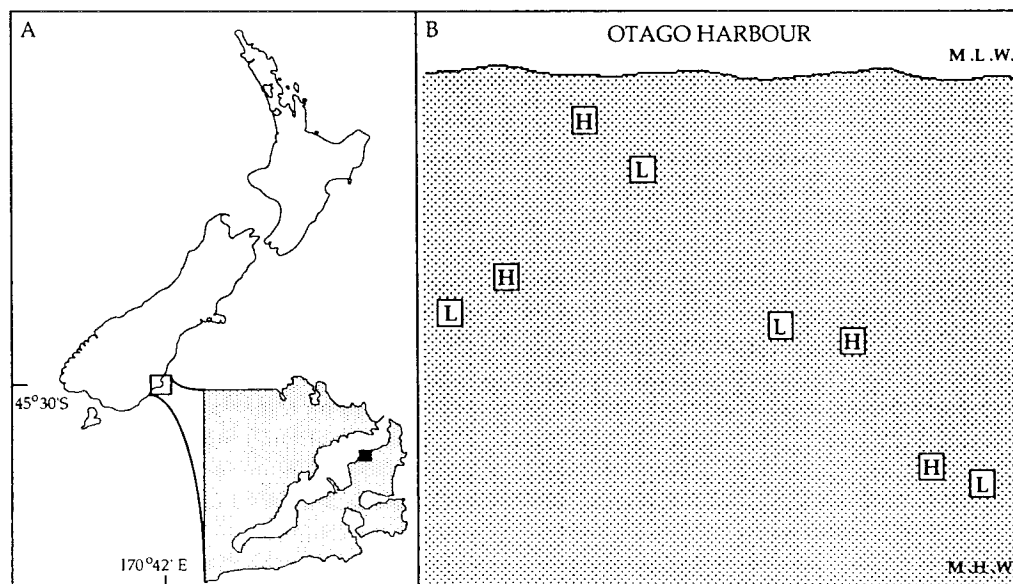

Fig. 1. (A) Location of the intertidal sandflat (■) in south-eastern New Zealand within Otago Harbour and (B) schematic layout of macrofauna sampling sites of low (L) and high (H) *Callianassa filholi* density (M.L.W. and M.H.W.: mean low and high water respectively)

Table 1. Results from the 2-way crossed ANOVA (factors: low and high *Callianassa filholi* density, time and interactions) for community measures and environmental factors at the intertidal sandflat (all seasons: November 1997 to June 1998) (Significant values in **bold**)

	Density		Time		Density × Time	
	F	p	*F*	p	*F*	p
Total number of species	1.1645	0.2823	11.685	**≤0.0001**	3.9886	**≤0.0001**
Total number of individuals	3.3706	0.0684	5.3303	**0.0016**	3.4851	**0.0175**
Evenness (J')	0.03467	0.8525	2.2814	0.0817	2.6278	0.0525
Seagrass biomass	1.0819	0.1796	2.0118	0.1148	0.47471	0.7004
Mean sediment grain size	0.49609	0.4823	4.9778	**0.0026**	0.65995	0.578
Organic content	2.0091	0.1585	0.90815	0.4388	1.4011	0.2449
Sediment sorting	0.2792	0.5980	3.7591	**0.0123**	0.19136	0.9022
Mound density	17.364	**0.0004**	10.083	**0.0002**	0.45351	0.7173
Mound volume	1.8916	0.1711	21.188	**≤0.0001**	0.25814	0.8554

high sediment turnover activity, whilst autumn and winter are times of low bioturbatory activity (Berkenbusch & Rowden 1999). On each sampling occasion, the number of mounds was recorded for each site and 5 haphazard cores (10 cm ∅, 10 cm depth) were collected. Adjacent to each macrofauna core, the volume of the closest mound (within 30 cm distance) was noted, and sediment cores were taken (3 cm ∅, 10 cm depth) for granulometry and organic content analysis.

Faunal samples were washed on 500 μm mesh and material retained on the sieve was fixed in 10% buffered formalin/seawater and stained with rose bengal. Macrofaunal specimens were identified to family level and thereafter to putative species (with the exception of Maldanidae). Seagrass material (*Zostera novazelandica*) was separated from faunal samples, dried (24 h at 70°C) and weighed. Sediment grain size was determined by sieving at 1 ϕ intervals from 1 mm to 63 μm (Buchanan 1984), and sediment sorting was ascertained using the program Rapid Sediment Analysis v. 7.1 (developed by the University of Waikato). Organic content was determined by loss of weight on ignition (4 h at 500°C).

Data analysis. Community composition was examined using the software package PRIMER, which has been specifically designed for the study of community structure (see Clarke & Warwick 1994). Univariate measures (total number of individuals, total number of species and index for evenness) were calculated utilising DIVERSE (Warwick et al. 1990a). Data were graphically assessed for normality (Zar 1984) and, due to non-significant block effects, differences in community measures and environmental parameters were tested by applying 2-way crossed ANOVA (involving ghost shrimp density and time as factors and including interactions). For multivariate analysis, a ranked triangular similarity matrix was derived based on the Bray-Curtis index on √-transformed data. For each sampling occasion, differences between sites within and between

low and high shrimp density grouping were tested by 2-way crossed ANOSIM permutations (Warwick et al. 1990b). Taxa contributing to the dissimilarities between density groupings were determined by the similarity percentages procedure SIMPER (Clarke 1993). The relationship between multivariate community structure and environmental parameters was investigated using the BIOENV procedure (Clarke & Ainsworth 1993). Environmental parameters used were seagrass biomass, mound density, mound volume, sediment grain size, sorting, and organic content (the latter 2 were log transformed, natural log). Mound density and mound volume were used as proxy measures for ghost shrimp bioturbatory activity.

It is important to note that one site was missed during sampling in April, resulting in a lower number of possible permutations and subsequently less power in the ANOSIM analysis. However, the remaining number of permutations was sufficient to accept the significance of detected differences for that sampling occasion.

RESULTS

Univariate analysis

The total number of species and total number of individuals changed significantly over time and between density groupings of *Callianassa filholi* over time (Table 1). Both community measures decreased in autumn and winter (April and June), particularly at sites of high *C. filholi* density (Fig. 2). Evenness did not change significantly between density groupings, or over time (Table 1, Fig. 2). Of the environmental parameters (Table 2), seagrass biomass and organic content showed no significant differences between density groupings or over time, but sediment grain size and sorting changed significantly over time, with the sorting coefficient being significantly higher for both den-

sity groupings in summer (January) (Table 1). Also, both mound density and mound volume differed significantly over time, with significant differences in mound density between sites of low and high ghost

shrimp density each season (Table 1). Values for mound density and mound volume were highest in summer, and both measures decreased markedly in autumn and winter (Fig. 3).
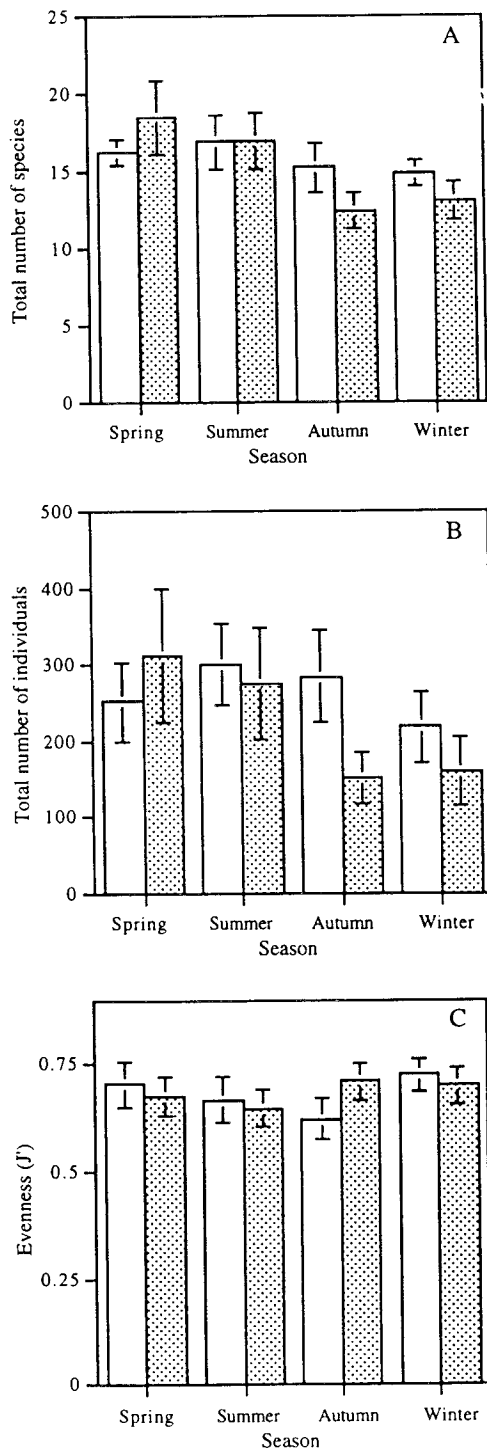

Fig. 2. (A) Mean values for total number of species, (B) total number of individuals, and (C) evenness for all seasons. Sites of low (open bars) and high (shaded bars) *Callianassa filholi* density (vertical bars = ±2 SE)
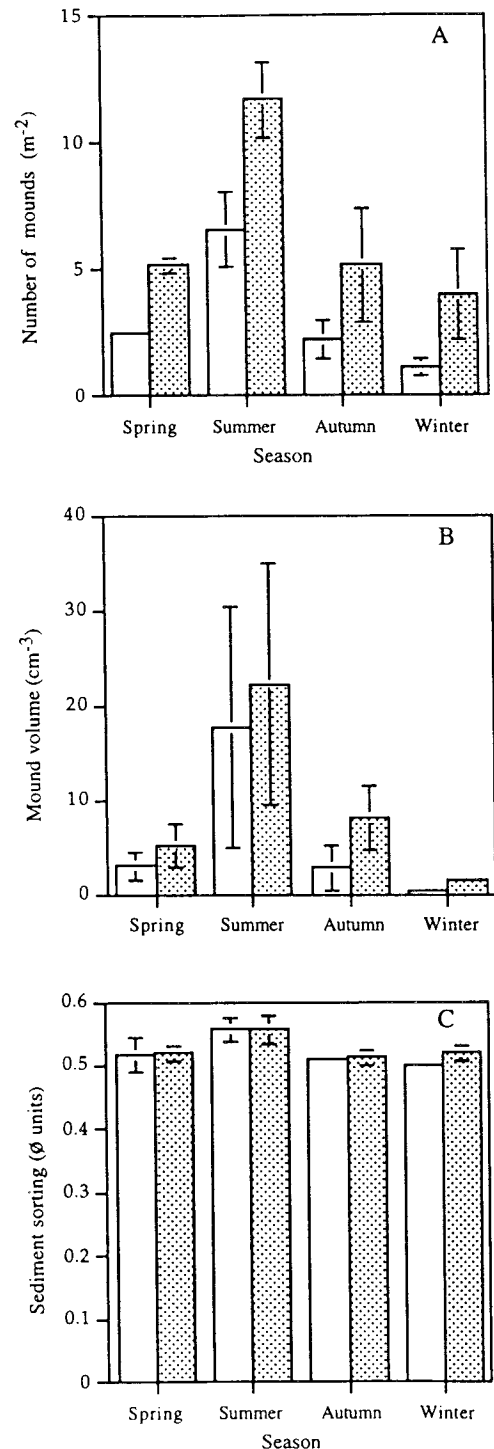
Fig. 3. (A) Mean values for number of mounds, (B) mound volume and (C) sediment sorting for all seasons. Sites of low (open bars) and high (shaded bars) *Callianassa filholi* density (vertical bars = ±2 SE)

Table 2. Summary of environmental parameters (mean values ±SE) from sites of low and high *Callianassa filholi* density for each sampling occasion

	Sites of low *Callianassa filholi* density				Sites of high *Callianassa filholi* density			
	Nov	Jan	Apr	Jun	Nov	Jan	Apr	Jun
Mound density (m⁻²)	2.50 ± 0.11	6.56 ± 0.67	2.23 ± 0.34	1.11 ± 0.17	5.16 ± 0.14	11.67 ± 0.66	6.85 ± 0.69	4.02 ± 0.79
Mound volume (cm⁻³)	3.07 ± 0.76	17.58 ± 6.36	2.82 ± 1.17	0.42 ± 0.18	5.19 ± 1.14	22.21 ± 6.32	8.08 ± 1.71	1.47 ± 0.34
Seagrass biomass (g)	1.62 ± 0.19	1.83 ± 0.32	1.44 ± 0.28	1.58 ± 0.17	1.54 ± 0.20	1.78 ± 0.25	1.24 ± 0.22	1.04 ± 0.18
Mean sediment grain size (φ)	2.37 ± 0.03	2.33 ± 0.01	2.38 ± 0.01	2.38 ± 0.01	2.38 ± 0.01	2.32 ± 0.02	2.38 ± 0.01	2.35 ± 0.01
Sediment sorting (φ)	0.516 ± 0.027	0.556 ± 0.018	0.509 ± 0.009	0.498 ± 0.009	0.519 ± 0.012	0.556 ± 0.208	0.512 ± 0.012	0.519 ± 0.011
Organic content (g)	0.002 ± 0.000	0.008 ± 0.001	0.001 ± 0.000	0.003 ± 0.001	0.008 ± 0.006	0.006 ± 0.001	0.032 ± 0.031	0.003 ± 0.000

Multivariate analysis

Two-way crossed ANOSIM permutation tests for each season indicated a significant difference in community structure between and, to a greater extent, within ghost shrimp density groupings (Table 3). Analysis of these differences each season using SIMPER showed dissimilarity percentages between low and high shrimp density sites and identified organisms contributing to those dissimilarities; out of a total of 56 species, 6 contributed the most (50%) to observed dissimilarities: the burrowing amphipod *Paracorophium excavatum* and the small bivalve *Perrierina turneri* appeared to have the most influence on dissimilarities throughout all seasons and consistently high ratio values ($\delta i/SD_{\delta i}$) confirmed their significance as discriminating species (Clarke 1993). Both species showed higher densities at sites of low ghost shrimp density (Table 4).

BIOENV results indicated that mound density and seagrass biomass were the main parameters explaining the macrofauna composition. Mound density accounted for maximum rank correlation in spring ($\rho_w = 0.266$), whilst seagrass biomass appeared to be the most important parameter in summer ($\rho_w = 0.378$). In autumn, the combination of both mound density and seagrass biomass gave the greatest rank correlation ($\rho_w = 0.435$), whilst mound density was the most significant factor in winter ($\rho_w = 0.435$).

DISCUSSION

Significant changes in mound density and expulsion mound volume, both monitored as proxy measures for spatial and temporal changes in sediment turnover activity, confirmed anticipated variation in *Callianassa filholi* bioturbation. Indeed, the study showed that the number and volume of mounds can be useful parameters for evaluating relative changes in bioturbation activity by a temperate callianassid shrimp (see also Berkenbusch & Rowden 1998, 1999).

Dissimilarities in community structure between sites of low and high *Callianassa filholi* density showed that although selected sites were part of one intertidal sandflat, benthic community composition altered in a relatively small, yet significant, way in space and time. Differences in community composition between areas of different shrimp density were evident over 10s of metres and months. Spatial and temporal patterns in shrimp density and sediment turnover have been shown to persist over the entire area of the sandflat which *C. filholi* inhabits (Berkenbusch & Rowden 1998 1999). The cause of changes in community structure appeared to be related to the bioturbatory activity of *C.*

Table 3. Results from the 2-way crossed ANOSIM test for differences in macrofaunal composition between sites of low and high *Callianassa filholi* density and between sites within each density grouping for each season (R: comparative measure of the degree of separation of sites) (significant values in **bold**)

Factor	November		January		April		June	
	R	p	R	p	R	p	R	p
Density (low vs high)	0.683	**≤0.001**	0.594	**≤0.001**	0.633	**≤0.001**	0.608	**≤0.001**
Sites	0.783	**≤0.001**	0.821	**≤0.001**	0.722	**≤0.001**	0.755	**≤0.001**

Table 4. Mean abundance (α) and dissimilarity (DS) of macrofaunal species averaged for and between high (α_H) and low (α_L) shrimp density sites for each season as calculated by SIMPER. Species are ranked in order of their percentage contribution ($\delta i\%$) to the average Bray-Curtis dissimilarity between both density groupings, including the ratio ($\bar{\delta}i/SD_{\delta i}$) and expressed as cumulative percentage ($\Sigma \delta i\%$) (cut-off to species list applied at 50%)

	Species	α_H	α_L	$\delta i\%$	Ratio	$\Sigma \delta i\%$
Nov, DS = 41.63%	*Perrierina turneri*	67.60	73.95	13.08	1.25	13.08
	Tanaidae 1	75.40	24.85	10.37	1.37	23.45
	Paracorophium excavatum	36.00	43.35	8.69	1.34	32.14
	Syllidae 1	46.55	23.75	7.14	1.36	39.28
	Enchytraeidae	11.90	18.10	5.29	1.18	44.57
	Tanaidae 2	6.45	3.90	4.47	1.49	49.04
Jan, DS = 43.75%	*Paracorophium excavatum*	45.65	74.25	12.72	1.54	12.72
	Perrierina turneri	43.55	91.60	12.69	1.52	25.41
	Syllidae 1	88.90	37.20	10.31	1.38	35.72
	Tanaidae 1	34.65	20.40	6.21	1.30	41.93
	Paracalliope novizealandiae	7.10	12.70	4.74	1.54	46.66
Apr, DS = 43.22%	*Paracorophium excavatum*	28.33	100.85	16.44	1.74	16.44
	Syllidae 1	37.53	59.35	11.54	1.39	27.98
	Perrierina turneri	33.80	44.15	9.90	1.37	37.88
	Enchytraeidae	2.93	20.25	7.53	1.27	45.42
Jun, DS = 43.45%	*Paracorophium excavatum*	40.65	50.45	13.92	1.44	13.92
	Perrierina turneri	35.10	41.85	11.04	1.38	24.96
	Enchytraeidae	7.75	29.15	9.68	1.49	34.64
	Syllidae 1	38.95	40.20	7.72	1.28	42.36
	Syllidae 2	5.45	10.65	6.02	1.36	48.38

filholi, the presence of *Zostera novazelandica* or a combination of both, depending on the season.

It can be assumed that the macrofaunal community as a whole is adapted to bioturbation as species of low tolerance to sediment turnover are likely to avoid sediments that contain large bioturbators (Woodin 1985). Such general adaptation of the benthic community is indicated at the present study site by the measure of evenness, for which no differences between sites of different shrimp density or over time were detected. Low values for the total number of species and total number of individuals in autumn and winter, particularly at sites of high *Callianassa filholi* density, can be explained by the cessation of recruitment which might compensate for the effect of disturbance during spring and summer. Multivariate dissimilarities in community structure occurred over a small scale on the study sandflat corresponding to bioturbation, implying that sediment disturbance exceeded tolerance levels at sites of high shrimp density.

Whilst few studies have investigated small-scale variations in bioturbation, Wilson (1981) noted that sediment disturbance by the large polychaete *Abarenicola pacifica* had a negative effect on the number of some tube-building species such as a small spionid polychaete. Also on a small spatial scale, the lugworm *Arenicola marina* and cockle *Cerastoderma edule* have been found to regulate the abundance of corophiid amphipods on tidal flats, but physical factors seemed to be more important over a large scale (Flach & de Bruin 1993). Following disturbance designed to stimulate a storm, patterns of macrobenthic recolonisation were different near (at the entrance) and away (>1 m) from burrows of the decapod crab *Macrophthalmus hirtipes*; although the same taxa were present, some common taxa, total number of taxa and total number of individuals were significantly less abundant at the burrow entrance, which has been attributed to the disruption caused by *M. hirtipes* walking in and out of the burrows (Thrush 1988). With respect to cal-

lianassid shrimp, Posey (1986) observed densities of several common macrofaunal species decreasing by an order of magnitude within a dense ghost shrimp bed in comparison to adjacent areas of low shrimp density. In agreement with these assessments of small-scale bioturbation, the findings of the present study imply that despite a general adaptation of the macrofauna community, bioturbation can change macrofaunal composition in small localised areas.

Spatial differences in community composition at the study site continued throughout all seasons, even though bioturbation declined significantly in colder months. Conversely, Myers (1977) found that the resilience of a spionid polychaete to a bioturbating holothurian, *Leptosynapta tenuis*, was linked to seasonal variation in sediment processing. That is, following recruitment in autumn, the spionids dominated numerically in winter, when sediment disturbance nearly ceased. Amphipods have been recorded to show seasonal variations in the effect of ghost shrimp density, exhibiting lower numbers when sediment turnover activity was high (Posey 1986). As a consequence, Posey (1986) speculated that natural reduction of bioturbation in winter, combined with migration by benthic fauna, produces a lesser impact on community structure. Whilst this would be reflected in smaller differences between areas of low and high shrimp densities, the present study controverts this view, as there was no significant alteration in impact on the macrofauna community with a decline in bioturbation. Instead, low sediment turnover activity during the colder months was accompanied by low abundance of macrofauna, so that the influence of bioturbation persisted at the same relative magnitude throughout the year.

Dissimilarities in macrofauna community structure were reflected in low abundances of both discriminating species *Paracorophium excavatum* and *Perrierina turneri* at sites of high shrimp density. Corophiid amphipods and bivalves have been shown previously to be susceptible to bioturbation. Sediment turnover by *Arenicola marina* and *Cerastoderma edule* led to a dramatic decrease in corophiid amphipods (Flach 1993), whilst the exclusion of ghost shrimp *Neotrypaea californiensis* resulted in a considerable increase in corophiid densities within 6 mo (Bird 1982). Sensitivity of corophiids to sediment turnover has been attributed to their tube-building behaviour, which is adversely affected by sediment disturbance (Brenchley 1981). Sediment disturbance can also have a deleterious effect on bivalves, interfering with feeding processes or causing (particularly small) bivalves to become disorientated within the sediment (Myers 1977, Murphy 1985). Furthermore, direct consumption and burial of newly recruited juvenile bivalves have been linked to

the exclusion of bivalves at sites where ghost shrimp were abundant (Peterson 1977).

Whilst bioturbation appears to have a significant and explainable influence on the spatial variation of macrofauna community composition, multivariate analysis identified seagrass (*Zostera novazelandica*) biomass as also contributing to the structure of the associated community. However, the underlying mechanism for the seasonal importance of *Z. novazelandica* is unclear as there were no significant changes in its biomass either between shrimp density groupings or over time. A possible explanation for its relative influence on macrofauna community composition could be related to seasonal variation in above-ground growth (i.e. shoots and leaves), depending on light and temperature. *Z. novazelandica* biomass was revealed by the BIOENV analysis to best explain community patterns during the optimum seagrass growing season (summer) and, to a lesser extent, in autumn (when both light and temperature declined). A connection between above-ground growth and infaunal community composition has been made by Webster et al. (1998), who attributed community differences in areas of low and high *Z. marina* densities to the number of leaves per shoot and shoot density. As seagrass beds generally have higher numbers of species and individuals than unvegetated areas (Bostroem & Bonsdorff 1997), an increase of above-ground growth of *Z. novazelandica* during summer possibly promoted the observed increase in these 2 community measures at sites of both density groupings in spite of high bioturbation rates. Therefore, *Z. novazelandica* may function as a 'buffer', in this case compensating for any possible negative effects of high sediment turnover activity by *Callianassa filholi* in warmer months.

Thus, it is possible from the present study to conclude that bioturbation by the ghost shrimp *Callianassa filholi* does impose small-scale spatial variation in macrofaunal community composition, and that any temporal variation is moderated by the seagrass *Zostera novazelandica*. However, natural experiments such as the present study cannot prove causality. Furthermore, it is evident from the values of the BIOENV analysis that bioturbation and seagrass biomass explain only part of the observed differences in community structure. Therefore, other factors must also be playing an important role. For example, predation has also been shown to impose small-scale differences in macrofaunal community measures for intertidal habitats (Thrush et al. 1994). In addition, the temporal changes in sediment sorting observed at the site hint at the role of physical parameters (e.g. waves). Such sediment variables have often been linked to large-scale patterns in community composition (Grant 1983). Flach & de Bruin (1993), who identified the impact of bio-

turbation on 2 amphipod species. attributed some of the impact to unknown factors operating over a large scale. Hence, it appears likely that bioturbation can be of primary importance on a small scale, whilst physical parameters are most likely to determine the macrofaunal community on a larger scale (Hall et al. 1993).

The identification of *Callianassa filholi* as an important bioturbator gives rise to the need for further studies; these could focus on the precise mechanism, possibly on an even smaller scale, by which spatial variation is imposed on the community composition (see Warwick et al. 1986). Furthermore, the present evidence suggests that *C. filholi* could be a singularly important species for structuring the sandflat macrofauna community — that is a keystone species (Paine 1966). Thus, the species requires further investigation, certainly considering the recent interest in applying the keystone species theory to soft sediments (Widdicombe & Austen 1998), and in the development of the ecosystem engineer concept (Jones et al. 1994), which allows for the assessment of the relative importance of various bioturbators to community structure.

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