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Journal of Experimental Marine Biology and Ecology, 216 (1997) 153–169

JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

Matching the outcome of small-scale density manipulation experiments with larger scale patterns an example of bivalve adult/juvenile interactions

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Abstract

Generalising or scaling up from small-scale experiments to larger areas is an important challenge for both ecology and conservation biology. This study describes a technique that attempts to meet this challenge by combining spatial mapping with small-scale process experiments. Specifically, we evaluate the density effects of large individuals (>15 mm shell length) of a tellinid bivalve (*Macomona liliana* Iredale) on macrofauna in 0.25 m^2 experimental plots within the natural density variation of large *Macomona* over a 12.5 ha site. By mapping the spatial distribution of large *Macomona* before conducting the experiment, we were able to identify homogeneous areas with different background densities of large *Macomona* and embed 22 experimental locations within the natural density-scape. Within each location, four experimental densities were added to plots from which all large macrofauna (>4 mm) had been previously removed. Macrofauna were sampled 22 days after the start of the experiment and significant negative treatment effects of high densities of large *Macomona* were identified by ANOVA for juvenile bivalves *Macomona* (<4 mm), *Austrovenus stutchburyi* (Gray) (<4 mm), the isopod

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PII S0022-0981(97)00094-4

Exosphaeroma falcatum Tattersall and the total number of individuals. Generalised linear models were then used to include the effect of background density variation of large *Macomona* in the analysis. Only *Austrovenus* (<4 mm) demonstrated a significant interaction between the background and experimental densities of large *Macomona*. This resulted from background densities of large *Macomona* having a significant effect on *Austrovenus* (<4 mm) in the two lowest density treatments only. Significant effects were detected only because we had planned the study to cover the various background densities of *Macomona*. The effect of experimental and background density variation of large *Macomona* on *Macomona* (<4 mm), *Exospheroma*, nemerteans and the total number of individuals were similar in direction and strength. Except for nemerteans, all relationships were negative, with low densities of macrofauna associated with high experimental and background densities of large *Macomona*. This implies that large-scale extrinsic factors (e.g., elevation, exposure to wave disturbance) are not the only features influencing the distribution of *Macomona* at the scale of the study site; intrinsic processes operating on smaller scales are also important. This scale-dependent response would not have been uncovered, had we not conducted a larger-scale survey in concert with the smaller-scale experiment.

Keywords: Adult/juvenile interactions; Bivalves; New Zealand; Sandflats; Scaling-up

1. Introduction

To achieve a mechanistic understanding relevant at larger ecological scales, it is essential to integrate small-scale experimental studies into the large-scale spatial mosaic. However, most ecological experiments are done in small areas over relatively brief time periods (Levin, 1988; Hairston, 1989; Kareiva, 1989; Eberhardt and Thomas, 1991) and the results are very rarely scaled up to meaningful spatial and temporal scales. The importance of integrating processes operating over different time scales and generating a broad perspective of the significance of individual studies has been demonstrated by Dayton and Tegner (1984). But still, the development of appropriate methods, allowing a combination of observations of system phenomena with experimentation on limited parts of the system, is virtually unexplored (Eberhardt and Thomas, 1991).

In this field study, we integrated the spatial distribution of a tellinid bivalve (*Macomona liliana*) with small-scale density manipulation experiments designed to identify adult/juvenile interactions. Our purpose was to increase our confidence in the generality (scaling-up) of the experimental results in space. An integrative process of testing the conclusions and inferences of earlier studies enabled us to further assess the generality of conclusions and to focus the experimental design. For example, low densities of adult *Macomona* (6 per 0.028 m^2; i.e., 214 per m^2) facilitated the recruitment of juvenile conspecifics during recolonization (Thrush et al., 1992). Strong interactions between adult *Macomona* and other macrofauna were also apparent when the predators of adult *Macomona* (eagle rays and shorebirds) were excluded from 4 m^2 plots (Thrush et al., 1994). In the latter study, increased densities of adult *Macomona* were associated with decreased densities of juvenile bivalves following recruitment. A third experiment directly assessed the influence of adults on recent recruits in sites with

different wave exposure and sediment grain size (Thrush et al., 1996). Adult *Macomona* significantly affected recently recruited conspecifics, but in opposite directions at each site: highest juvenile densities were associated with high adult densities in muddy-sand but with no adults in sand. Using this information we predicted that, in the sandy sediments of this study, densities of adult *Macomona* typical of those found in high density patches (e.g., 20 per 0.0415 m^2 used in Thrush et al., 1996; i.e., 482 per m^2) would have a negative effect on the density of juvenile conspecifics over small spatial scales.

It was not clear how changes in the size of experimental plots or habitat characteristics would influence our results. A number of factors could result in changes to the outcome of adult/juvenile interactions. For example, mechanisms operating on different scales to those encompassed by an experiment might influence results. Bivalve densities in the vicinity of an experimental plot might directly or indirectly affect the outcome of an experiment through influences on predator densities, post-settlement bivalve mobility, food supply or mortality of adult bivalves (e.g., crowding, parasitism). Apart from helping to extrapolate the findings of small-scale experiments, integrating pattern and process studies can also be used to help identify other processes, such as scale-dependent predation that could influence local biotic interactions.

We addressed the issues of scaling-up experimental results and the possibility that processes operating on different spatial scales confound results by conducting small-scale density manipulations of adult *Macomona* embedded within the natural, larger-scale spatial distribution of the bivalve. Specifically, we test the following hypotheses: (1) there are no density dependent effects of adult *Macomona* on the density of juvenile conspecifics and other macrofauna; (2) large-scale density variation of adult *Macomona* within the study site does not confound experimental effects and (3) locating experimental plots within the natural density variation of adult *Macomona* does not increase our confidence in scaling up experimental effects. Additional workshop studies helped in the study design and interpretion. For instance, preliminary sampling of *Macomona* spatial distributions (Hewitt et al., 1997) determined appropriate scales on which to map physical and biological variation within the sandflat (Legendre et al., 1997).

2. Methods

2.1. Study site

The experiment was conducted on the extensive sandflats adjacent to Wiroa Island in Manukau Harbour (37 °01.3′S; 174 °49.2′E), New Zealand. The Wiroa Island sandflat is about 1.8 km wide and has a shallow gradient (0.097 °). Surface topography is characterised by areas of ridges and runnels (bar and trough bedforms 2–20 cm height, 8–30 m wavelength), wave generated ripples (1–2 cm height), small patches (< 10 m diameter) of eelgrass (*Zostera* sp.) and, during the summer months, feeding pits (usually 20–30 cm in diameter and 10–15 cm deep) created by eagle rays (*Myliobatis tenuicaudatus* (Hector)). The surface sediments comprise 0–3% gravel (primarily shell hash), 92–97% sand and 3.5% mud by dry weight. The macrofaunal community is

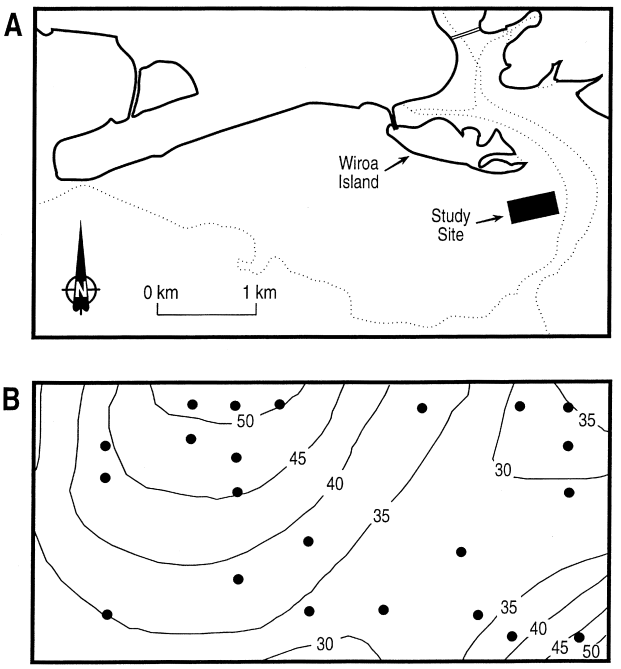

Fig. 1. (A) Location of the study site on the Wiroa Island sandflat, Manukau Harbour. (B) Contour lines representing the mapped density of *Macomona* > 15 mm within the study site (see Legendre et al., 1997 for details); dots mark the location of the 22 experimental sites on the *Macomona* density-scape.

dominated in terms of both abundance and biomass by bivalves (Pridmore et al., 1990). A site of 250 m × 500 m was chosen to encompass scales of variation in sediment characteristics and bivalve densities typical of this habitat (Fig. 1(a)); detailed analysis of the biological and physical spatial variation within the study site is presented in Legendre et al. (1997).

2.2. Embedding experimental design into the Macomona density-scape

To map the density of large *Macomona* (i.e. individuals > 15 mm long) the study site was divided into 200, 25 m × 25 m grid cells. Sample locations were selected randomly within each grid cell and marked by small wire pegs. In a few instances, sample location was changed slightly to avoid local features such as eagle ray pits and small *Zostera* patches. At each location, three cores (13 cm diam. × 15 cm deep) were collected within a 0.25 m^2 quadrat and sieved (500 μm mesh) to extract macrofauna. Once the cores had been removed, the remaining sediment in the quadrat was excavated to a depth of 15 cm and sieved (4 mm mesh) to collect large bivalves. The density of large *Macomona* in each of the 200 sample locations was based on the sum of individuals (> 15 mm) collected in the 3 cores and in the excavated sediment. This sampling strategy enabled us to capture spatial variability with separation between sample locations ranging from

5–530 m ($\bar{x}$ inter-sample distance: 201 m), and enabled us to describe the density variation of large *Macomona* within the 12.5 ha study site (Fig. 1(b)).

Except for the 60 cells that formed the perimeter of the study site, a mean density ($\pm$SD) of large *Macomona* was determined for each cell, based on the density in that cell and in the 8 adjoining grid cells. This defined the ''neighbourhood'' density for 140 locations within the study site. Neighbourhood densities ranged from low ($>$26–36 individuals per 0.25 m^2), through medium ($>$36–46 individuals per 0.25 m^2) to high ($>$46–56 individuals per 0.25 m^2) density. Twenty-two grid cells representative of a variety of densities were chosen as locations for the experiment units (Fig. 1(b)). The locations chosen were spread throughout the study site, deliberately avoiding areas with high variability (i.e. standard deviation) in the neighbourhood density of adult *Macomona*. Locations were separated by between 15–435 m, with a mean inter-location distance of 204 m. Restated in statistical terms, neighbourhood density was treated as a ratio-scale (regression-type) variable, rather than a nominal (ANOVA-type) variable.

There are several advantages to this experimental design. Firstly, the results from the experimental plots are representative of the entire study area. The 22 experimental sites are representative of the 200 grid sampling stations because they form a doubly stratified selection among the 200 sites, along the scale of large *Macomona* densities. The first stratum defines the three neighbourhood densities while the second stratum spreads out the samples within each group. The original 200 grid cell sampling locations are themselves a statistically representative sample of the whole 12.5 ha (because of the stratified-random sampling design). As a consequence, the results of the analysis of the 22 sites can be extrapolated and applied to the 12.5 ha area. Secondly, the full and quantitative use of the survey data in the experimental design enables a tighter coupling of experiment to survey. Thirdly, the technique differs from simple stratification in that each grid point is assigned a neighbourhood density, rather than becoming a unit within a larger block that is assumed (often without assessment) to be of homogeneous density. We also can avoid the edges of patches and grid cells with high density variation, thereby reducing potential confounding effects of heterogeneities in larger scale blocking. Fourthly, neighbourhood densities can be calculated at several scales, other than just the adjacent grid squares.

2.3. Experimental design

At each of the 22 chosen grid cells, an experimental unit was placed within 1.5 to 2 m of the original survey sample location. Each unit consisted of four 0.25 m^2 plots that were separated by about 3 m, and marked by wire pegs. Each plot was excavated to 15 cm depth, the sediments were sieved (4 mm mesh) to remove large bivalves and shell fragments and the sieved sediments were immediately returned to the plot. Previous studies (Thrush et al., 1991, 1992; Commito et al., 1995) suggested that changes to sediment chemistry associated with the excavation and sieving of sediment would be undetectable after 4 tidal cycles. Bivalves collected during this process were counted and the mean density of large *Macomona* from the 4 plots was defined as background density for the subsequent experimental analyses. Experimental plots were not sur-

rounded with sub-surface netting or other material to restrict the lateral movement of infauna, because we were concerned that exposure of netting by sediment movement could modify flow over the plots (Snelgrove et al., 1995). A pit-fall trap (5 cm diam. × 30 cm deep PVC tube) was buried in the centre of each plot and capped to prevent it from filling with sediment. When not in use (see below) the top of the pitfall trap was buried 2–3 cm below the sediment surface.

At each location, plots were haphazardly assigned to one of four experimental treatments, i.e. the addition of 0, 15, 50 or 120 *Macomona* (15–40 mm shell length) to sediments from which large bivalves had been removed. All experimental plots were established in one low tide period (25 January 1994). All *Macomona* added to experimental plots were collected from the vicinity of the experimental site and marked with non-toxic spray paint. In each experimental plot, the appropriate number of *Macomona* were placed on the sediment surface, in approximately regular arrays, and allowed to burrow. Individuals which did not bury themselves within about 1 h were replaced; by the time the tide covered the individual experimental plots all of the introduced *Macomona* had successfully burrowed into the sediment.

2.4. Observations and sampling

The experimental plots were visited on 26 and 27 January to assess rates of re-appearance of marked *Macomona* at the sediment surface, as well as the numbers of *Macomona* (marked and unmarked) left by predatory birds (mainly South Island Pied Oystercatchers *Haematopus ostralegus finschii* Martens), and whether the pitfall traps were causing sediment scour. These observations, and counts of eagle ray pits in the vicinity of the experimental plots were continued over the course of the experiment (see Cummings et al., 1997; Hines et al., 1997).

Pitfall traps were used to sample mobile epibenthic invertebrates on four occasions (25 and 27 January, and 5 and 9 February). On each date, the traps were positioned so their tops were flush with the surrounding sediment and their caps were removed. The traps were left to sample for one high tide period. On the following low tide, traps were emptied of their contents, re-capped and pushed into the sediment so their tops were buried 2–3 cm below the sediment surface. The contents of the traps were sieved (500 μm mesh) and the animals were preserved in isopropanol, identified and counted. The number of epibenthic predators and the total number of epibenthic invertebrates collected in pit fall traps were analysed by three-way ANOVA. Abundance data were transformed ($\ln(x + 0.01)$). Date and location were treated as random factors, treatment as a fixed factor and all two-way interaction terms were included in the model.

The experiment was sampled on 16 February 1994, 22 days after its initiation. A 0.25 m^2 quadrat was placed over each plot and aligned with the corner pegs. Three core samples (13 cm diam. × 15 cm deep) were taken and the sediment remaining in the quadrat (0.21 m^2) was then excavated to a depth of 15 cm and sieved (4 mm mesh). A 15 cm wide perimeter band was also excavated around each plot to estimate the density of marked *Macomona* that had moved out of the experimental plots. This excavated sediment was sieved (4 mm mesh) and the marked *Macomona* were counted. Preliminary trials revealed that excavation of wider perimeter bands around the plots

failed to collect marked *Macomona*. Core samples were sectioned into 0–2 cm and >2–15 cm depth fractions. The surface 0–2 cm of sediment was preserved (70% isopropanol and 0.1% Rose Bengal in seawater) prior to elutriation in super-saturated sucrose solution. The elutriate was then sieved on a 250 μm mesh to extract recently settled macrofauna. Preliminary trials using this technique demonstrated greater than 95% efficiency in capturing macrofauna when contrasted with sorting sediment residues under a dissecting microscope. The remainder of each core was sieved (500 μm mesh) to extract macrofauna and the residues fixed in 70% isopropanol and 0.1% Rose Bengal in seawater. Macrofauna were identified to the lowest taxonomic level practical and counted. Bivalves <10 mm shell length were measured using a dissecting microscope, camera lucida and digitizing pad; larger specimens were measured to the nearest 0.1 mm using electronic callipers.

We assessed the influence of large *Macomona* on 2 separate size classes (<4 mm and 4–15 mm) of conspecifics and 3 size classes (<4 mm, 4–10 mm and >10 mm) of the cockle *Austrovenus stutchburyi*. In all analyses, density estimates for bivalves >4 mm are based upon the number in each 0.25 m^2 quadrat, while for smaller bivalves and other species of macrofauna density estimates are based on the sum of the 3 cores (i.e. a total area of 0.04 m^2) collected from within each 0.25 m^2 plot.

2.5. Statistical analyses

Although this experiment was not designed in a classical way, we initially analysed the effect of treatment on the density of recruits in experimental plots using ANOVA, a commonly used technique. Prior to performing ANOVA, data were $\ln(x + 0.01)$ or, more commonly, rank transformed (Iman and Conover, 1983) to reduce violations of assumptions of normality (Shapiro Wilk test) and homogeneity of variance (F max test). Each of the 22 locations was considered a block containing one replicate of each treatment. Treatment and location were considered fixed and random factors, respectively. When significant treatment effects occurred, we identified differences between treatments (*a posteriori* comparisons) using SNK multiple comparison tests for $\ln(x + 0.01)$ transformed data and Tukey's rank sum test for rank transformed data.

Generalised linear models (McCullagh and Nelder, 1989; Crawley, 1993) were then used to increase the flexibility and generality of the evaluation of data (Schneider, 1992). Specifically, this enabled us to: use treatment densities as a continuous rather than categorical factor; use neighbourhood density of large *Macomona* as a continuous factor and include an interaction term for these two continuous factors. Also, given the nature of our data (counts with many 0's and 1's), the ability to use Poisson or negative binomial error structures is likely to produce more appropriate statistical models. Models were developed using a normal, Poisson (quasi-likelihood specification), or negative binomial (quadratic specification) error structure and a log link function (Proc Genmod (SAS Institute Inc., 1993)). Plots of standardised Pearson's and deviance residuals were used to evaluate fit (Bajdik and Schneider, 1991). While models based on different error structures gave similar results in terms of significance of effects, fits of the negative binomial models were consistently better and only these results are presented. In the

generalised linear models, information on larger scale variations in the density of large *Macomona* was used, i.e. location was replaced with background density as a continuous factor. At this stage treatment was still considered a fixed factor and a treatment–background interaction term was included in the model. If a significant interaction term was found ($P < 0.1$), the effect of the background density of large *Macomona* was examined at each treatment level. If no significant interaction term was obtained, data were re-analysed as a response surface. Treatment levels were replaced by the average of the initial and the final density of all large *Macomona* for each plot. Both experimental and background densities of large *Macomona* were thus treated as continuous factors.

3. Results

The background density of large *Macomona* recorded during the preliminary mapping were highly correlated with the density estimates obtained during the initial excavation of the experimental plots ($r = 0.88$, $P = 0.0001$). This indicates that the initial mapping was effective in predicting local densities of large *Macomona*.

Macomona feeding tracks were observed during the experiment in all plots to which *Macomona* were added. Feeding tracks were also observed in the plots from which bivalves (>4 mm) had been initially removed; probably a result of some bivalves washing into the plot during the excavation or the lateral migration of *Macomona* into the plots. Surface sediment in the plots was indistinguishable from that of the surrounding sediment 2 days after the start of the experiment; by this date the redox potential discontinuity had re-established at 2–3 cm depth. Over the first two days of the experiment a total of 43 dead marked *Macomona* (i.e. 1% of those added) were found near the 22 experimental locations. The distribution of these dead *Macomona* did not relate to either treatment or location and was probably due to handling disturbance. Predation by shorebirds was noted in the study site but was not focused on experimental plots (see Cummings et al., 1997) and eagle ray feeding pits were never observed in experimental plots.

Pitfall traps failed to collect any large mobile invertebrates on the first two sampling occasions (26 and 27 January) because high rates of sediment transport filled the traps with sand. On 5 and 9 February, in contrast, relatively little sand and few mobile epifauna (e.g., 1–2 individuals per trap) were collected. Species found in the traps included crabs (*Halicarcinus whitei* (Miers), *Helice crassa* Dana and *Hemigrapsus edwardsi* (Hilgendorf)) and gastropods (*Zeacumantus lululentus* (Kiener), *Cominella glandiformis* (Reeve), *Bulla quoyi* Gray and *Diloma subrostrata* (Gray)). Not surprisingly, given the low number of individuals collected, the number of predators and total numbers of individuals collected in the traps were not significantly related to experimental treatment or location within the study site (ANOVA, data $\ln(x + 0.01)$ transformed: Total number of individuals: treatment $P = 0.523$, location $P = 0.316$, date $P = 0.203$, treatment $*$ location $P = 0.363$, date $*$ treatment $P = 0.926$, date $*$ location $P = 0.457$; Number of predators: treatment $P = 0.788$, location $P = 0.102$, date $P = 0.936$, treatment $*$ location $P = 0.543$, date $*$ treatment $P = 0.800$, date $*$ location $P = 0.699$).

3.1. Main experimental results

Densities of large *Macomona* in experimental plots changed during the experiment (Table 1); these increased in the two low density treatments where experimental densities were less than background, but decreased in the two high density treatments although only the highest experimental density exceeded background density. These density changes reflect mortality and migration of large *Macomona* over the course of the experiment. As the numbers of unmarked Macomona (>15 mm) that moved into the zero additions plots were similar to those recorded in other treatments (GzLM, negative binomial errors: initial experimental density $P = 0.214$; background density $P = 0.0640$; interaction $P = 0.0943$) it does not appear that loss of marking paint appreciably confounded analysis of movement. Initial GzLM analysis showed no significant interaction between treatment and background densities of large *Macomona* (GzLM negative binomial errors: $P = 0.8939$). Subsequent analysis demonstrated the only factor to significantly influence the density of large *Macomona* that moved out of the experimental plots was the initial experimental density (GzLM negative binomial errors: $P = 0.0001$).

By the end of the experiment density still differed significantly among each of the four nominal levels ($F_{3,85} = 98.98$, $P = 0.0001$) and resulted in a range of large *Macomona* densities more similar to the range apparent in the ambient sediment. The treatment levels used in the subsequent analyses were therefore based on the average of the initial transplanted *Macomona* density and the density of all large *Macomona* (i.e. >15 mm) collected at the end of the experiment (Table 1).

Animals were considered to be sufficiently abundant to warrant statistical analyses if they exhibited a mean of one individual per core in all treatments, or a mean of greater than four individuals per core in at least one treatment. The most abundant animals to colonise the experimental plots were juvenile bivalves (*Macomona*, *Austrovenus* and *Cyclomactra ovata* (Gray)) and two small epibenthic crustaceans (the isopod *Exosphaeroma falcatum* and the cumacean *Colurostylis lemurum* Calman). The only abundant worms were nemerteans.

Preliminary statistical analyses that included the effect of variation in background density of large *Macomona* simply as part of a categorical variable based on location, demonstrated significant treatment effects on the density of *Macomona* (<4 mm), *Austrovenus* (<4 mm), *Exosphaeroma* and the total number of individuals colonising the experimental plots (Table 2). Generally, densities of these colonists decreased with

Table 1
Changes in density of large *Macomona* in experimental plots during the experiment

Transplant density	Final mean density	±SE	Treatment density average over the course of the experiment
0	17.8	1.9	8
15	21.7	1.3	18
50	38.9	2.0	45
120	63.4	3.0	94

Table 2
Results of ANOVA used to identify significant treatment effects irrespective of background density

Source	df	Sum of squares	F	$P > F$	df	Sum of squares	F	$P > F$	df	Sum of squares	F	$P > F$
	Macomona liliana (<4 mm) {$\ln(x+0.01)$}				*Macomona liliana* (4–15 mm) {rank}				*Austrovenus stutchburyi* (<4 mm) {rank}			
Treatment	3	1.761	5.24	0.0027	3	1500.423	0.92	0.4367	3	5721.023	4.50	0.0063
Block	21	8.720	3.71	0.0001	21	18 829.870	1.65	0.0664	21	24 239.000	2.72	0.0012
Error	63	7.057			63	33 716.619			63	26 697.977		
	Austrovenus (4–10 mm) {rank}				*Austrovenus stutchburyi* (>10 mm) {rank}				*Cyclomactra ovata* {$\ln(x+0.01)$}			
Treatment	3	2143.578	1.92	0.1350	3	2795.764	2.33	0.0833	3	1.156	1.62	0.1943
Block	21	29 098.528	3.73	0.0001	21	20 844.173	2.48	0.0030	21	10.487	2.10	0.0127
Error	63	23 029.838			63	24 831.590			63	15.015		
	Exosphaeroma falcatum {rank}				Nemerteans {rank}				*Colurostylis lemurum* {rank}			
Treatment	3	29 784.375	3.80	0.0001	3	49.386	0.05	0.9856	3	1096.431	0.84	0.1943
Block	21	3123.341	2.79	0.0479	21	35 083.875	4.96	0.0001	21	27174.375	2.96	0.4788
Error	63	2342.784			63	21 222.738			63	27522.193		
	Total number of individuals {$\ln(x+0.01)$}				Number of taxa {$\ln(x+0.01)$}							
Treatment	3	1.075	4.22	0.0088	3	0.017	0.2	0.8937				
Block	21	5.980	3.36	0.0001	21	1.029	1.76	0.0434				
Error	63	5.345			63	1.749						

Note: The particular data transformation applied is shown in parenthesis.

increasing density of large *Macomona*, and the multiple comparison tests revealed significant contrasts between the high and low density treatments (Fig. 2). Significant location effects were also exhibited by all variables, except *Macomona* (4–15 mm) and *Colurostylis*.

Generalized linear modelling enabled us to link the density-dependent experimental effects of large *Macomona* with the background density of large *Macomona*. A

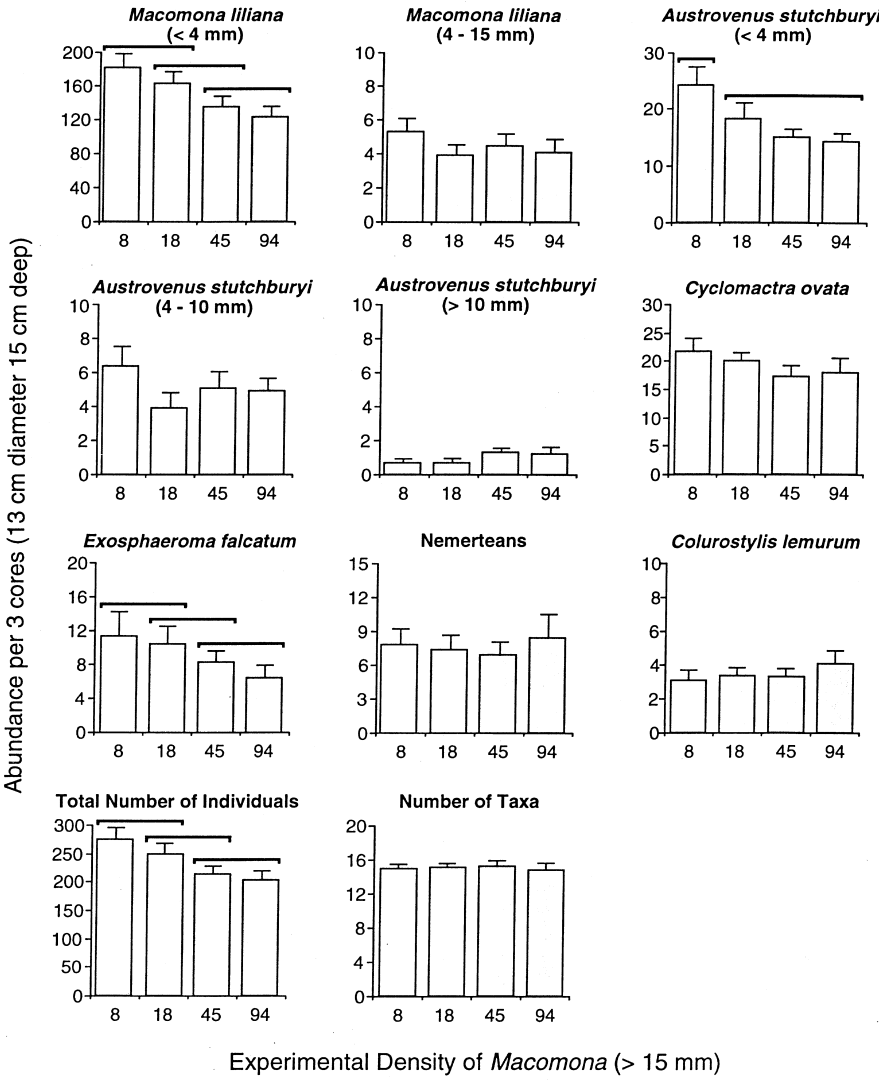

Fig. 2. The density of colonists in the four experimental treatments. Lines above histograms show the results of multiple comparisons tests conducted when significant differences were detected using ANOVA (see Table 1). Treatments connected by the same line are not significantly different.

Table 3
Generalised linear model analyses on the effects of *Macomona* treatment densities (categorical variable) and background densities of large *Macomona* (continuous variable) on macrofauna

	Deviance/df	Pearsons χ^2 deviance/df	Treatment level *P*	Background density *P*	Interaction *P*
Macomona (<4 mm)	1.033	0.979	0.9274	0.0003	0.9632
Macomona (4–15 mm)	0.993	0.987	0.2015	0.2920	0.1524
Austrovenus (<4 mm)	1.032	0.867	0.0105	0.0898	0.0481
Austrovenus (4–10 mm)	1.033	0.811	0.8218	0.0001	0.8659
Austrovenus (>10 mm)	0.972	0.872	0.4896	0.2451	0.6970
Cyclomactra ovata	1.099	0.988	0.6672	0.0001	0.7240
Exosphaeroma falcatum	1.046	0.992	0.4041	0.0073	0.4722
Nemerteans	1.003	1.049	0.4409	0.0001	0.5253
Colurostylis lemurum	1.138	0.878	0.5799	0.1532	0.4781
Total number of individuals	0.957	0.851	0.7368	0.0057	0.9344
Number of taxa	0.466	0.454	0.9565	0.1888	0.9620

Note: The degrees of freedom for each model are 80, with 3 for treatment, 1 for background density and 3 for the interaction term. *P* values given are type 3 χ^2 probabilities.

significant interaction term between treatment and background densities of large *Macomona* was identified only for *Austrovenus* (<4 mm) (Table 3). Analysis of the relationship between *Austrovenus* (<4 mm) and background density of large *Macomona* at each of the four treatment levels revealed no significant effect of background density in the two highest treatments (Table 4). However, negative relationships were apparent for the two low experimental densities, indicating that in these treatments lower numbers of *Austrovenus* (<4 mm) were found in areas with high background densities of large *Macomona*.

All the variables, except *Austrovenus* (<4 mm), were re-analysed as response surfaces of the continuous variation in average experimental density and background density of large *Macomona* (Table 5). This analysis identified a significant experimental effect for nemerteans, with higher nemertean densities associated with high experimental densities. Except for nemerteans, all significant relationships with experimental density were negative, indicating that increased densities of large *Macomona* in 0.25 m^2 experimental plots decreased the density of colonists. In each case where a significant relationship with experimental density was found, a significant relationship of similar

Table 4
The effect of background density of large *Macomona* on *Austrovenus* (<4 mm) within each treatment level

Treatment density	df	χ^2 prob	Slope
8	1	0.0153	−0.0002
18	1	0.0128	−0.0003
45	1	0.1739	
94	1	0.4753	

Note: Each treatment density is averaged over the course of the experiment (see Table 1). If the type 3 χ^2 probability value (χ^2 prob) is <0.05 then the estimate of the slope parameter (Slope) is given.

Table 5
Generalised linear model analyses on the effects of experimental *Macomona* densities (continuous variable) and background densities of large *Macomona* (continuous variable)

	Deviance/df	Pearsons χ^2 deviance/df	Experimental density *P*	Slope	Background density *P*	Slope
Macomona (<4 mm)	1.014	0.974	0.0022	−0.0002	0.0003	−0.0001
Macomona (4–15 mm)	1.051	1.085	0.4607		0.5019	
Austrovenus (4–10 mm)	1.017	0.811	0.8230		0.0001	+0.0029
Austrovenus (>10 mm)	0.989	0.889	0.1399		0.1737	
Cyclomactra ovata	0.935	0.844	0.2294		0.0001	−0.0072
Colurostylis lemurum	1.102	0.894	0.2416		0.0968	
Exosphaeroma falcatum	1.029	1.016	0.0389	−0.0003	0.0029	−0.0014
Nemerteans[b]	0.936	1.192	0.0377	+0.0001	0.0001	+0.0004
Total number of individuals[a]	1.017	0.905	0.0066	−0.0001	0.0026	−0.0002
Number of taxa	0.447	0.436	0.9505		0.2144	

[a] transformed by logs.
[b] transformed by squaring.
Note: Models are as described in Table 3, except that instead of using a mean of each plots' large *Macomona* density averaged over the duration of the experiment (see Table 1) as a categorical variable, individual values for each plot were used. The degrees of freedom for each model are 80, with 1 each for background and experimental densities. If the type 3 χ^2 probability value (χ^2 prob) is <0.05 then the estimate of the slope parameter estimate (Slope) is given.

magnitude and in the same direction was also found with the background density of large *Macomona*. *Cyclomactra* and *Austrovenus* (4–10 mm) both revealed significant relationships with the background density of large *Macomona* but not with experimental density. Direct comparison of the estimates of the treatment and background density parameters of large *Macomona* (Table 5) must be interpreted cautiously because the range of experimental densities (averaged over time) is larger than that found in the site. Taking this into account it is apparent that the treatment effect is smaller than that caused by background *Macomona* density. However, the surfaces shown in Fig. 3 indicate the difference between treatment and background *Macomona* density is less than one order of magnitude. Except for nemerteans, macrofaunal densities are decreased due to increased experimental and background density of large *Macomona*.

4. Discussion

Epibenthic invertebrate predators and surface sediment disturbers were relatively uncommon throughout the experimental site (authors' personal observations) and based on animals collected in the pitfall traps they do not appear to be targeting particular experimental treatments. However, without information on the susceptibility of individual species to collection by pitfall traps, it is important to be cautious in interpreting these results. Although Hines et al. (1997) demonstrate that eagle rays tend to feed in large areas (>10 m^2) of high *Macomona* density, we never observed ray pits in the 0.25 m^2 experimental plots. Similarly, despite the high potential rates of consumption of large *Macomona* by South Island Pied Oystercatchers, there was no evidence that the

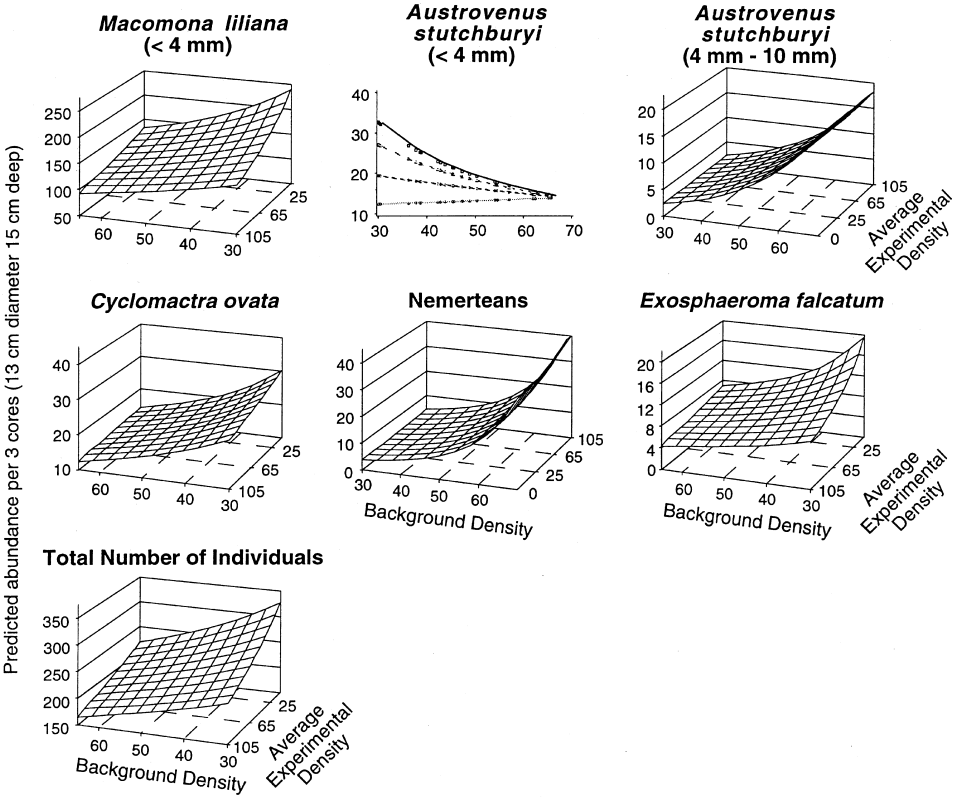

Fig. 3. Predicted trend surfaces relating the effect of background and experimental density variation of large *Macomona* using generalised linear modelling (see Table 5). As *Austrovenus* <4 mm demonstrated a significant background–treatment interaction (Table 4) the effects of background densities of large *Macomona* are plotted separately for each treatment level. Treatments are ordered from the lowest to highest density starting at the top of the graph.

birds were targeting experimental plots with high *Macomona* densities (Cummings et al., 1997).

Although our experiment was not confounded by the direct effects of predation, embedding the experimental plots into the natural density-scape provided an opportunity to identify whether experimental plots were being indirectly affected by predators and other spatially related processes that could cause variations in experimental responses around the study site. Such scale-dependent response could not be identified without conducting a larger-scale survey in concert with the experiment. Significant treatment–background interaction terms in the generalized linear models indicate the possibility of such large-scale processes confounding treatment effects. Although treatment $*$ block interactions in classical ANOVA could indicate the same phenomena, by utilizing information on the ambient density-scape of large *Macomona* we could identify sources of confounding that related to background *Macomona* density or possible co-variates. In

this study the only significant response to interaction occurred in the analysis of *Austrovenus* (<4 mm). There was no significant effect of the background density of large *Macomona* on the number of *Austrovenus* (<4 mm) in the high density treatments, but in the two low density treatments fewer *Austrovenus* (<4 mm) were found in areas where the background density of large *Macomona* was high. If, by chance, the experiment had been conducted only in an area with high numbers of large *Macomona* we would have been unlikely to identify any effects on small *Austrovenus*. Significant effects were detected only because we had planned the study to cover the various natural ambient densities of *Macomona*.

Our results are consistent with some predictions of earlier studies conducted on the Wiroa Island sandflat. For example, Thrush et al. (1994) and Thrush et al. (1996) found that high densities of large *Macomona* had strong negative effects on the density of juvenile conspecifics and other macrofauna. However, we found no indication of facilitation by large *Macomona* at low densities as described in Thrush et al. (1992). The density used in Thrush et al. (1992) equated to 54 individuals per 0.25 m^2, well within the density range exploited in the present study. If responses had changed from facilitation to inhibition with increasing density of large *Macomona*, we would not have observed a monotonic inhibitory response. Inconsistency in the outcome of these experiments could relate to differences in the background density of *Macomona* or differences in the size of experimental plots (Whitlatch et al., 1997). Collectively, however, all the studies of bivalve interactions on the Wiroa Island sandflat demonstrate consistent negative effects of high densities of *Macomona* on most common macrofauna.

Analysis of *Macomona* spatial structure and its relationships with various physical, hydrodynamic and sediment properties failed to identify a significant relationship between adult and juvenile *Macomona* at the scale of the study site (Legendre et al., 1997). This suggests that the relationship between adult and juvenile *Macomona* may simply be a result of large-scale environmental variables affecting their distributions. However, the direction of the effects of experimental and background densities of large *Macomona* on juveniles were similar. This, together with the larger effect of background density variation (as indicated by slope parameter estimates in the generalized linear modelling), suggests that the effect of background density effect incorporates an interaction between adult and juvenile *Macomona* as well as other larger scale processes. Scale-dependent patterns need not be generated solely by processes operating at the same scale as the pattern (Schneider, 1994a). The results of our experiment imply that large-scale extrinsic factors (e.g., elevation, exposure to wave disturbance) are not the only features influencing the distribution of juvenile *Macomona* at the scale of the study site; intrinsic processes operating on smaller scales are also likely to be important. In addition, the results of Hewitt et al. (1997) emphasise local biological relationships nested within the larger-scale physical gradients, highlighting the need for multi-scale studies of ecological and environmental processes.

To our knowledge this is the first study that has attempted to directly link the distribution of infauna to processes operating on the cm–hundreds of metres scales. To draw the most accurate conclusions, experiments need to be conducted over as wide a range of conditions likely to influence the variables of interest as possible. Identifying variations in habitat conditions (sand vs. mud, vegetated vs. non-vegetated) can usually

be done subjectively, but encompassing the range of infaunal densities within a habitat is far more difficult and requires some form of preliminary sampling. In this study, the preliminary mapping helped by defining the density-scape of adult *Macomona* within an apparently homogeneous habitat. We were able to describe the potential for confounding factors within the study site and perform complementary studies that assisted with the interpretation of our experimental results (Cummings et al., 1997; Hines et al., 1997; Legendre et al., 1997; Turner et al., 1997).

Experimental designs and analytical techniques used in this study greatly increase our ability to integrate the results of small-scale experiments with the larger scale patterns within the study site. It should be recognised, however, that in generalising from local biotic interactions to the study site we are linking processes operating on spatial scales that differ by at least 3 orders of magnitude. As illustrated by the scale-dependent effects of predators in this system (Cummings et al., 1997; Hines et al., 1997; Whitlatch et al., 1997), we may expect variability in both estimates of density and the importance of processes to change as a function of scale (Schneider, 1994b; Bellehumeur and Legendre, 1997). The statistical scale-up from the experimental plots to the study site and from the study site to the Wiroa Island sandflat (as we initially determined the study site to be biologically representative of the sandflat) is simple compared to larger-scale extrapolations. To successfully generalise to other sandflats or harbours, we need knowledge of how local interactions vary with changes in important extrinsic physical variables. Nevertheless, we have demonstrated that local biotic interactions can play a role in affecting the distribution of macrofauna over large areas of sandflat.

Acknowledgements

We thank Ken Heck and Mick Keough for comments on this paper and Jared Rigg for his awesome help with field work and sample sorting. We thank Auckland Airport Security for access to the study site. This research was made possible by support from NIWA-NSOF and FRST-CO1517.

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