THE GENERALITY OF FIELD EXPERIMENTS: INTERACTIONS BETWEEN LOCAL AND BROAD-SCALE PROCESSES

Simon F. Thrush,[1,3] Judi E. Hewitt,[1] Vonda J. Cummings,[1] Malcolm O. Green,[1] Greig A. Funnell,[1] and Michelle R. Wilkinson[2]

[1]*National Institute of Water and Atmospheric Research, P.O. Box 11-115, Hamilton, New Zealand*
[2]*National Institute of Water and Atmospheric Research, P.O. Box 109-695, Newmarket, Auckland, New Zealand*

Abstract. Linking the results of localized field experiments to generalities about the role of specific processes is essential in ecology. Comparative studies conducted at multiple locations enable the general importance of processes to be assessed. However, spatial or temporal variation in the strength of local ecological relationships frequently makes it difficult to draw general conclusions, as increasing the extent of a study is likely to increase the physical and biological heterogeneity. To unravel the influence of differences in wave climate on local ecological interactions among adult and juvenile sandflat bivalves, an experiment was conducted at three sites in each of three harbors in the North Island of New Zealand. The selected sites covered a range of wind–wave exposures but were all mid-intertidal sandflats with macrobenthic communities dominated by bivalves. Four treatments were used: additions of 0, 15, 45, and 110 adults of the tellinid bivalve *Macomona liliana.* At each site a DOBIE wave gauge was used to provide time-series data on wave orbital speed at the seabed over the 35-d duration of the experiment. Significant experiment × location interactions indicated site-dependent variation in the strength and direction of treatment effects. However, multiple regression models based on site environmental characteristics were very successful in explaining differences between sites in the strength of experimental treatment effects (66–99% of the variance explained). We used the cube of the orbital wave velocity at the seabed (U_b^3) as an index of energy dissipation by waves. Both the site average and maximum U_b^3 were important variables explaining location-dependent treatment effects. Average U_b^3 increased the strength of the negative effects of experimental additions of adult *Macomona* on juvenile bivalves, presumably by increasing the opportunity for juvenile bivalves to be resuspended by small waves and transported away from areas with high adult densities. Maximum U_b^3 decreased the strength of the experimental effects, probably by increasing the purely passive transport of juveniles with sediment bedload and thus obliterating patterns in the distribution of juvenile bivalves relative to adult *Macomona.* Hence, different aspects of the wave climate influenced adult–juvenile interactions in different ways. Ambient density of adult *Macomona* around the experimental sites was also an important factor. This multisite experiment confirmed the importance of local adult–juvenile interactions and suggested ways in which these interactions are influenced by local environmental characteristics. Where the influence of such broad-scale variables can be identified, linking broad-scale information to small-scale studies that identify mechanisms can increase the generality of ecological experiments.

Key words: adult–juvenile interactions; bivalves; broad-scale processes; generality in field experiments; intertidal sandflats; local processes; Macomona; *meta-analysis; New Zealand; postlarval movement; scaling up; wave climate.*

INTRODUCTION

Ecological systems are naturally heterogeneous and there is growing evidence that the processes which generate natural variability operate over different scales of space and time (e.g., Dayton and Tegner 1984*a,* Levin 1988, Wiens 1989, Thrush 1991, Levin 1992, Legendre 1993, Giller et al. 1994, Menge et al. 1997*a*). Conducting field experiments is very time consuming and, consequently, intensive field experiments are usually conducted over a very restricted spatial extent (i.e., at

few sites) making it difficult to empirically assess generality (Kareiva and Andersen 1988, Hairston 1989, Eberhardt and Thomas 1991, Schneider et al. 1997). For example, the importance of the mechanisms identified in a field experiment may change under circumstances that are beyond the spatial and temporal extent of individual field studies. Developing techniques to generalize the results of intensive field experiments, or to recognise the limits of generality, is one of the many scaling problems facing field ecologists attempting to make population and community ecology more predictive (Thrush et al. 1997*a*).

To develop a mechanistic understanding of how ecological communities are structured, it is important to

recognize how processes change from place to place and time to time. Beck (1997) discusses the problem of overgeneralizing the results of field experiments conducted at few locations and advocates random selection of experimental sites to extend the theoretical domain over which the results are valid. However, experiments conducted at a number of locations frequently demonstrate location $\times$ treatment interactions. In other words, there is some process (or combination of processes) influencing the direction and strength of the treatment effects for which location is an adequate surrogate. If we randomly select sites and ignore quantifiable variation between them, simply demonstrating a location $\times$ treatment interaction does not advance our understanding of how processes operating over different scales interact. Unless the appropriate covariables have been measured, we can not explain what is causing this variation in experimental effects from place to place. This limits our ability to make broad-scale predictions about the relative importance of local ecological processes.

One way to overcome problems with spatial variation in the importance of local ecological processes that result from interactions with phenomena of broader scale is to place sites along gradients of factors that are likely to modify treatment effects (Keddy 1991). This approach has a long history in ecological studies of rocky-shore environments (e.g., Dayton et al. 1970, 1971, Menge 1976, Underwood et al. 1983). More recent research, nesting comparative experiments within the broader scale variation among sites, has led to a better understanding of the interaction between local biotic processes and regional oceanographic variability (e.g., Dayton 1994, Menge et al. 1994, 1997a, b, Estes and Duggins 1995).

The potential predictive advantage of using a gradient approach is that, if effects of broad-scale processes can be statistically modeled as a monotonic gradient, then the role of the broader scale processes in affecting local ecological processes can be understood. If the effect of the broad, gradient-scale processes modifies the intensity rather than the direction of the local processes, then multiple regression can be used to analyze effects across sites. Meta-analysis can be used in this circumstance and also when broad-scale effects change the direction of the local processes (Rosenthal 1991, Gurevitch and Hedges 1993). However, given the number of factors that potentially play a role in influencing ecological processes, choosing the factor to use as a gradient may not be simple. Some basic knowledge of how the system functions (and some luck) is required.

In marine benthic systems, a variety of interactions between hydrodynamic and benthic community processes have been demonstrated. Broad-scale relationships between larval abundance and current patterns have been identified (e.g., Butman 1987, Roughgarden et al. 1987). Relationships between coastal upwelling and increased benthic and pelagic primary productivity can influence both the competitive interactions among macrophytes and the growth rates and density of benthic suspension feeders (e.g., Dayton and Oliver 1977, Menge et al. 1994, 1997a, b, Menge 1995, Tegner et al. 1997). More localized phenomena associated with the influence of benthic boundary flows on settlement cues and feeding behavior are also well documented (e.g., Eckman 1979, Butman et al. 1988, Andre et al. 1993, O'Riordan et al. 1995). Extreme physical disturbance due to storm induced waves can also influence benthic communities (Rees et al. 1977, Dobbs and Vozarik 1983, Dayton and Tegner 1984b, Denny 1995, Posey et al. 1996). In soft-sediment marine systems there is growing evidence that waves generated by less extreme events are also important, influencing the abundance and transport of benthic diatoms (Miller et al. 1984, Grant 1985, Emerson 1989, Miller 1989, Delgado et al. 1991), feeding behavior of infauna (Turner and Miller 1991, Bock and Miller 1995), and habitat topography (Dolphin et al. 1995). Wind-waves are the short and choppy waves or ripples common within harbors and estuaries that are created by local wind conditions. These waves are an important determinant of postlarval transport (Emerson and Grant 1992, Commito et al. 1995a, b). Postlarval dispersal is an important phenomenon for many soft-sediment organisms, transporting individuals over spatial scales of meters to 100's of kilometers (Beukema and de Vlas 1989, Armonies 1992).

In marine soft-sediment habitats, adult–juvenile interactions (sensu Woodin 1976) often influence population and community structure and this local ecological process is likely to be influenced by postlarval transport. There is some consensus in the literature for high densities of adult deposit-feeding bivalves to have negative effects on juveniles (Olafsson et al. 1994). However, some studies have found positive effects or no significant effects (e.g., Hines et al. 1989, Ahn et al. 1993, Thrush et al. 1996a). Methodological differences between studies (e.g., laboratory vs. field based studies, different spatial or temporal scales, levels of replication) make it difficult to assess the strength of adult–juvenile interactions from literature reviews. The most rigorous synthesis can be achieved by formal meta-analysis based on experiments of identical design conducted at different locations in space and/or time, combined with measurements of key environmental parameters that are likely to constrain local biotic interactions.

Our work on intertidal sandflats has directly or indirectly demonstrated the negative effect of high adult densities of the deposit-feeding tellinid bivalve *Macomona liliana* on juvenile conspecifics and some other members of the infaunal community (Thrush et al. 1994, Hewitt et al. 1997a). We have demonstrated the role of adult–juvenile interactions in the mesoscale (1–10^5 m²) distribution of bivalves (Thrush et al. 1997a,

b). These studies were conducted on one large sandflat (~1.8 km wide) off Wiroa Island in Manukau Harbour, New Zealand. However, Thrush et al. (1996*a*) demonstrated negative interactions between adult and juvenile *Macomona* on this sandflat, and positive interactions in an identical experiment conducted simultaneously on an adjacent muddy-sand flat, and inferred these differences were related to sediment characteristics and/or hydrodynamic conditions. Thus, to generalize from sandflat to sandflat and harbor to harbor we need to understand how local ecological processes interact with processes operating on broader scales. Our previous studies have emphasized the importance of wind-waves in enabling juvenile bivalves to be moved with the sediment bedload (Commito et al. 1995*b*, Hewitt et al. 1997*a*). We have demonstrated that juvenile *Macomona* actively move from unfavorable areas that are contaminated by a pesticide (Pridmore et al. 1991) or contain high densities of the spionid polychaete *Boccardia syrtis* (Cummings et al. 1996). Furthermore, the flux of juvenile bivalves on the sandflat is positively correlated with the density of adult *Macomona,* at least on calm days (Turner et al. 1997). These factors have an important influence on the mesoscale (1–10^5 m^2) distribution of infauna (Legendre et al. 1997).

In this paper, we attempt to unravel the interaction between broad-scale differences in wave climate and the strength of the relationship between adult *Macomona* and juvenile bivalves. We predict that the strength of this relationship, as revealed by small-scale density manipulation experiments, will be influenced by wave climate. Based on our previous studies, we predict that waves facilitate the development of distribution patterns of high densities of juvenile bivalves in areas of low densities of adult *Macomona,* by enabling juvenile bivalves to be transported out of unfavorable areas. However, if the intensity of wave activity on the sandflat becomes too extreme, then waves will transport juvenile bivalves en masse, thus obliterating patterns in the distribution of juvenile bivalves relative to adult *Macomona.* Thus, we also predict that information on wave climate at each site over the course of the experiment will enable us to explain variation in the strength of the local interaction between these adult and juvenile bivalves.

METHODS

Study sites

To assess the strength of the relationship between adult *Macomona* and juvenile bivalves in relation to environmental characteristics, experiments were conducted in three harbors in the North Island of New Zealand (Manukau, Tauranga, and Whangapoua; Fig. 1a). Three sites were chosen to reflect a range of wave conditions within each harbor (Fig. 1b–d), but as we could not predict the weather over the course of the

experiment, we could not predictably rank sites in terms of short-term wave exposure. These harbors have similar morphologies, with extensive intertidal sandflats dissected by subtidal drainage channels. Manukau Harbour is situated on the west coast and connects to the Tasman Sea. This harbor is exposed to the prevailing southwesterly winds. Tauranga and Whangapoua harbors are situated on the east coast and connect to the Pacific Ocean. Both are exposed to the northeast and Tauranga is also exposed to southerly winds. The harbors differ in size and thus potential wave fetch (Table 1, Fig. 1b–d). Under typical conditions we would expect the three harbors to be ordered along a gradient of increasing wave exposure from Whangapoua to Tauranga to Manukau. All sites were mid-intertidal sandflats, with macrobenthic communities dominated by bivalves.

Experimental setup

The experiment was set up over four days, 28–31 January 1997. Separate field teams operated in each harbor to enable sites to be set up simultaneously, thus avoiding possible confounding effects of different experimental start times. At each experimental site, five blocks (separated by ~25 m) were established (Fig. 1e). Each block occupied an area of ~4 m^2 and was composed of four (0.5 × 0.5 m) experimental plots (Fig. 1f). In each block, experimental plots were randomly assigned to one of four treatments: additions of 0, 15, 45, and 110 individuals of the tellinid bivalve *Macomona liliana* (20–40 mm long) per 0.25 m^2. These densities of adult *Macomona* reflect the natural density range previously identified on sandflats and are similar to those used in previous experiments (Thrush et al. 1996*a,* 1997*b*).

To establish the experimental plots, a 0.25-m^2 metal quadrat, with 15 cm deep sides, was inserted into the sediment. The sediment within the quadrat was excavated to a depth of 15 cm and sieved through a 4-mm mesh. The *Macomona* retained on the sieve were identified and, for those sized >15 mm long (i.e., adults), counted and preserved. The average counts (from the four excavated plots comprising a block) of adult *Macomona* were subsequently used to represent the ambient density of adults around each experimental block. To prevent the horizontal migration of adult bivalves, the walls of the excavated experimental plot were then lined with 10-mm plastic mesh. The sieved sediment was placed back in the excavated plot and the metal quadrat was removed. The four corners of the plot were marked with small metal pegs and the appropriate number of *Macomona* were then added to the plot. All four plots within a block were completed before the next block was started. At least one block from each site was set up on each day. On the last day of the experimental setup, a sample of the top 2 cm of the sediment surface was taken from the center of each block at each
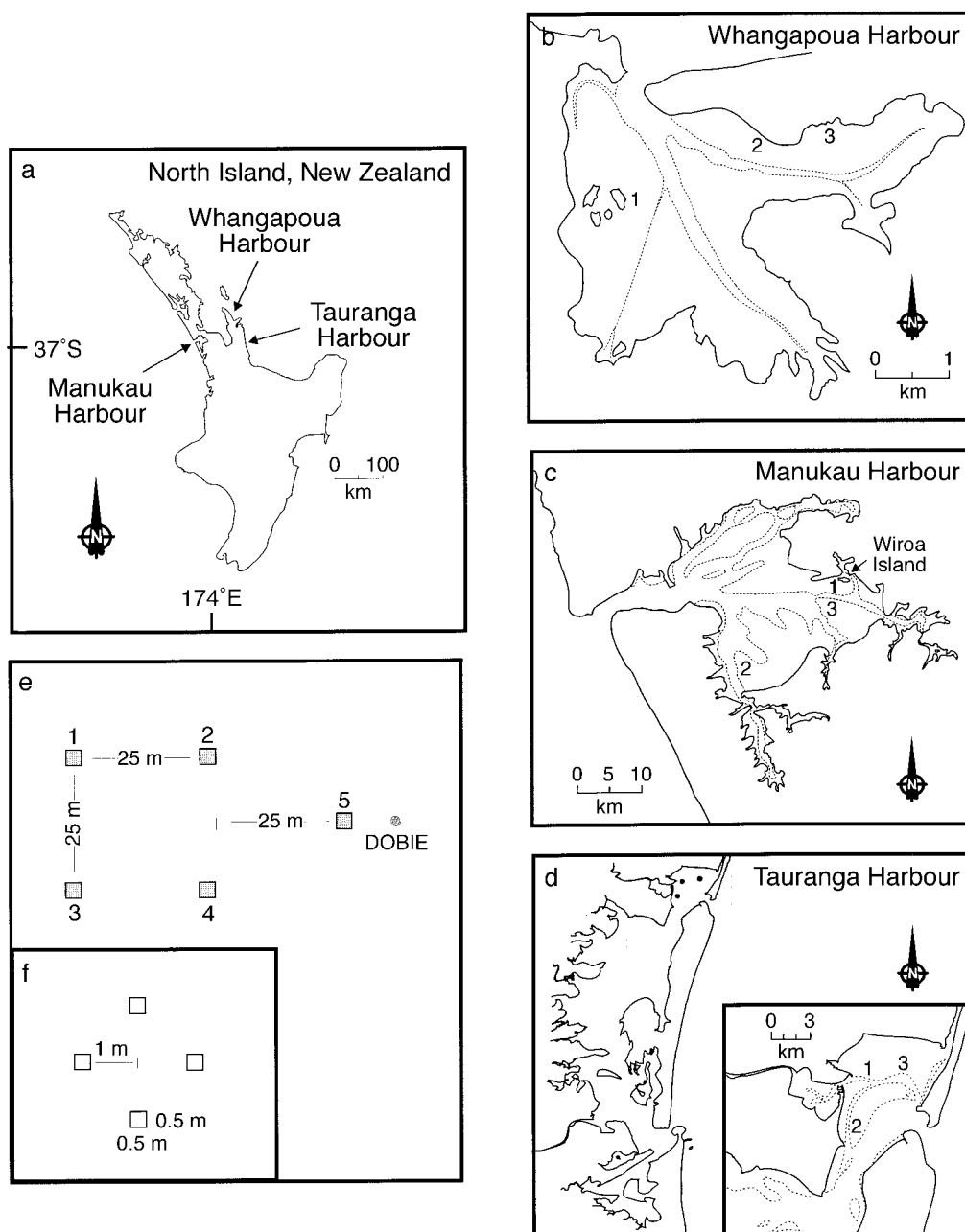
FIG. 1. (a) North Island of New Zealand showing the location of the three harbors; (b–d) experimental sites within harbors; (e) spatial arrangement of experimental blocks within a site; (f) spatial arrangement of experimental plots within a block.

TABLE 1. General characteristics of Manukau, Tauranga, and Whangapoua harbors in New Zealand (based on Hume and Herdendorf [1993]).

Characteristic	Harbor		
	Manukau	Tauranga	Whangapoua
Area, including islands (km^2)	368	196	13
Intertidal area (as percentage of total area)	42	92	83
Spring tide range (m)	3.8	1.6	1.7
Spring tidal prism (m^3)	9.18×10^8	2.27×10^8	8.5×10^6

site to assess ambient sediment grain size and organic carbon content.

To assess the initial disturbance created by excavating the experimental plots, we collected 2 cm diameter × 2 cm deep surficial sediment samples for chlorophyll *a* analysis and measured depth from the sediment surface to the apparent redox potential discontinuity zone (RPDZ). These samples were collected 4 d after the experimental setup began, from inside and outside of the zero-*Macomona* treatment plot in the first block to be completed at each site. One chlorophyll *a* sample and five measurements of the apparent RPDZ were made in and out of each plot. At this time, notes were also made on the presence of sand ripples, epifaunal gastropods, crabs, and any dead *Macomona* on the surface of the experimental plots at each site.

The experiment was sampled 35 d after its initiation (on 3–6 March 1997). Experimental plots were sampled to estimate the density of bivalves. Experimental blocks were sampled in the same order as they had been established. A metal quadrat was inserted into the sediment around the outside of the netting that lined the walls of the plot. One core sample (13 cm diameter, 13 cm deep) was collected from the center of the plot. The top 2 cm of sediment collected in the core was sieved on a 250-μm mesh to extract recently settled bivalves that are found near the sediment surface. The rest of the core was sieved on a 500-μm mesh. The sieved samples were preserved in 70% isopropanol containing 0.1% rose bengal in seawater. The sediment remaining in the quadrat was excavated to a depth of 15 cm and sieved on a 4-mm mesh, and the *Macomona* were counted and sized.

In the laboratory, the material from each core retained on the 250-μm mesh was elutriated in supersaturated sucrose solution to remove juvenile macrofauna and sediments were sorted to remove larger macrofauna. Preliminary trials at each site using this technique demonstrated >94% efficiency in capturing macrofauna when contrasted with sorting sediment residues under a dissecting microscope. The material from the rest of the core that was retained on the 500-μm mesh was also sorted to remove macrofauna. All macrofauna were identified and counted. Bivalves <4 mm long (hereafter referred to as small juveniles) were measured using a dissecting microscope, a camera lucida, and a digitizing pad; larger specimens were allocated to one of two size classes: 4–15 mm (large juveniles) and >15 mm (adults).

Chlorophyll *a* was extracted from sediments by boiling in 95% ethanol, and the extract processed using a spectrophotometer. An acidification step was used to separate degradation products from chlorophyll *a* (Sartory 1982). To determine surficial sediment grain size, samples were digested in 6% hydrogen peroxide for 48 h to remove organic matter, and dispersed using the detergent calgon (0.5% [mass : volume] sodium hexametaphosphate). A Galai particle analyzer (Galai Cis

−100, Galai productions, Migdal Haemek, Israel) was used to measure sediment grain size (percentage volume at 0.5-mm intervals for particles from 2.00 to 0.001 mm diameter). Cumulative percentage volumes were calculated for the medium sand, fine sand, and silt-clay sediment fractions.

Wave data

We used a DOBIE wave gauge (NIWA Instrument Systems, Christchurch, New Zealand) at each of the nine sites to measure waves and water depth (and thus immersion time) over the duration of the experiment. DOBIE consists of a pressure sensor interfaced to a controller/logger and a battery power supply, all of which is contained within a small pressure case. DOBIE measured pressure in bursts, with each burst consisting of 2048 data points at a sampling interval 0.2 s. The interval between bursts was 30 min.

When waves are absent the pressure sensed by DOBIE is composed of two parts: hydrostatic pressure, which is due to the mass of the overlying water column and which is proportional to the height of the water column above the DOBIE, and atmospheric pressure, which is due to the mass of the overlying atmosphere. When waves are passing overhead, there is an additional fluctuating pressure associated with the waves. The fluctuating pressure decreases in amplitude with depth below mean water level, and the rate of decrease depends inversely on wave period (e.g., Madsen 1976). Thus, pressure fluctuations under short-period waves decay faster with depth than do fluctuations under long-period waves, which means that long-period waves are more readily detected at depth.

Because the time average of the fluctuating pressure is zero, the burst-averaged water depth, $\bar{h}$, can be calculated from the raw pressure simply by subtracting the atmospheric pressure and time averaging as follows:

$$\bar{h} = \frac{\overline{p(t) - p_a}}{\rho g} + z_p \qquad (1)$$

where $p(t)$ is the burst time series of pressure measured by DOBIE, p_a is atmospheric pressure, ρ is water density, g is acceleration due to gravity, z_p is elevation of the DOBIE above the bed (actually 0 cm in all cases), and the overbar indicates a burst average. To estimate wave statistics, DOBIE first manipulated $p(t)$ as follows. Atmospheric pressure was removed from each $p(t)$ and each resultant time series of hydrostatic-plus-fluctuating pressure was then converted to a time series of sea-surface elevation, which is defined as the water level relative to mean water level (sea-surface elevation is negative during the passage of a wave trough and positive during passage of a wave crest). The conversion was accomplished by applying linear wave theory, which describes the relationship between pressure and sea-surface elevation. In essence, linear wave theory is used to ''unattenuate'' the pressure signal, and there-

by reconstruct the surface wavetrain that would cause the observed pressure fluctuations. All of the wave statistics were then calculated by DOBIE directly from each burst time series of sea-surface elevation (''surface wavetrain''), as follows.

Real waves are irregular, meaning that the wavetrain is composed of many different constituent waves with different heights and periods and traveling in different directions. Average measures of wave properties are required to characterize the irregular wavetrain. For wave height, DOBIE uses significant wave height, H_{sig}, which is the average height of the highest 33.3% of the waves in a burst, and which was estimated as 1.42 times the variance of the sea-surface elevation (e.g., Longuet-Higgins 1952). Significant wave height is commonly used to characterize wave height in engineering applications, and has been shown to equal what the casual observer would call ''wave height''. For wave period, DOBIE uses mean spectral period, $\bar{T}$, which is estimated using Longuet-Higgins's (1975) definition. This definition is not greatly affected by the details of the wave irregularity, unlike some alternative choices including peak spectral period and mean zero-downcrossing period. Wave height and period can then be combined to estimate orbital speed at the bed (U_b). U_b is the maximum horizontal orbital speed generated by the wave motion during the wave cycle, at the top of the wave boundary layer, within which wave-orbital speed decays to zero down to the actual bed. DOBIE uses linear wave theory to estimate the U_b generated by a wave of height H_{sig} and period $\bar{T}$ in water depth $\bar{h}$.

A good measure of wave activity at the seabed is the rate at which wave energy is dissipated by bed friction, D_e, which is equivalent to the rate at which work is done on the bed by the waves. D_e is proportional to the cube of U_b and thus doubling U_b causes an eight-fold increase in dissipation and ''wave activity.'' Note that ''wave activity'' does not imply the existence of a threshold in the same way that sediment entrainment does. In the case of wave-energy dissipation, the constant of proportionality, f_e, varies with bed type (Nielsen 1992). For flat beds, f_e depends on sediment grain size, and for rippled beds it depends on bedform steepness and height. However, U_b^3 alone can be used as a reasonably accurate comparative indicator of D_e among sites if the differences in f_e among sites are much smaller than differences in U_b^3.

Since the bed sediments and bedforms at all of our sites were similar but exposure to winds varied greatly, we expect a priori that differences in f_e among sites will be much smaller than differences in U_b^3 and we are therefore justified in using U_b^3 as a comparative indicator of D_e among sites. We quantified wave activity by calculating the following statistics: (1) total U_b^3, as a measure of total wave energy dissipation over the duration of the experiment; (2) average U_b^3 (i.e., total U_b^3 divided by number of bursts when waves were present), as a measure of the typical wave energy dissipated

on the sandflat; (3) maximum U_b^3 (measured in a single burst), as a measure of the largest wave event; and (4) maximum/average U_b^3, as a measure of the variability in wave energy dissipation over the duration of the experiment. We defined ''waves present'' as those times when $U_b > 1$ cm/s, which is approximately the level of resolution of the DOBIE. We also calculated the percentage of the total time waves were present at the site, the percentage of the time waves were present when the site was immersed and the total number of bursts when waves were present.

Statistical analyses

Paired t tests were used to test the significance of differences in sediment chlorophyll a content and depth of the apparent RPDZ in and out of the zero-*Macomona* treatment, over all sites, 4 d after the experiment started.

Most statistical analyses were performed within a generalized linear modeling framework (McCullagh and Nelder 1989, Crawley 1993); this approach increases the flexibility and generality of the evaluation of data, particularly where non-normal errors occur (Schneider 1992). Initially a model with normal error structure and no data transformations (i.e., standard ANOVA) was run for each variable. Model fit was evaluated by visual inspection of half-normal plots of residuals together with plots of residuals vs. predicted values. If this model type was inappropriate, a model with Poisson error structure and log transformation was evaluated. If this model proved inappropriate, a model with negative binomial error structure and a log transformation was evaluated. Results are presented for model types that resulted in the best fit. In all cases, use of different model types did not affect the significance of results at the $P = 0.05$ level.

To test whether there was a significant interaction between location and the effect of the adult *Macomona* density manipulation on the juveniles of the three most common species of bivalves (i.e., *Macomona liliana, Austrovenus stutchburyi,* and *Nucula hartvigiana*), the harbor and the sites nested within a harbor were treated as categorical variables. Mean densities of adult *Macomona* recorded from each treatment at the end of the experiment differed slightly from the initial transplant density. Therefore, an average of the initial transplant density and the final density was calculated on a plot by plot basis, and this average was used as a continuous variable in all analyses.

Multiple regression was used to assess the role of wind-wave climate and other site dependent environmental variables in influencing the strength of local biotic interactions between adult *Macomona* and juveniles of the three common species of bivalve. The analyses were performed using SAS software (SAS Institute 1993, SAS/Insight 1993). Meta-analysis usually involves regressing P values (or r values for regressions) from a variety of studies, and then assessing

whether the significance of individual tests, or the variability within different tests, can be explained by other factors. Usually this is all that can be done when summarizing over studies with different methodologies (e.g., different density manipulations). However, in our study, the identical experiments at each site enabled us to use the slope of the regression of manipulated *Macomona* density on density of juvenile bivalves at each site (i.e., the actual estimate of the size of the effect due to the manipulation of adult *Macomona* density) in the meta-analysis. Invariably some of the slope estimates will not be significantly different from zero. However, if nonsignificant slope estimates are small, which was the case with our data (see Table 4), this does not cause problems with the interpretation of the meta-analysis. In order to develop these meta-analytical models, the regression model used from each site must be similar. We evaluated a number of model types with raw data and log or exponential transformations and different error structures (normal, Poisson, negative binomial). We also included polynomial functions to indicate any nonmonotonic responses. After visual examination of the best fit of these different models, we used the regression model for each dependent variable that gave the best results for most of the sites.

RESULTS

Post-experiment site conditions

Even though all sites were selected to represent mid-intertidal sandflats of similar morphology, the data derived from DOBIE revealed that the sites exhibited quite different hydrodynamic conditions (Table 2). Sites in Manukau showed the greatest range of immersion times, while Tauranga sites were generally immersed longest and Whangapoua sites were generally immersed for the least time. Site 2 in Manukau recorded the largest waves, while site 1 in Whangapoua recorded the smallest (i.e., 40 cm high with 9-s period and 10 cm high with 10-s period, respectively). Examination of the wave climate at each site measured by the time waves were present and the statistics based on our index of wave energy dissipation (U_b^3), revealed some interesting differences between sites. Sites most frequently experiencing waves were site 3 in Manukau, site 2 in Tauranga, and site 1 in Whangapoua. Sites 2 and 3 in Whangapoua experienced a consistently low wave climate (i.e., low maximum/average U_b^3, Table 2). Although the maximum U_b^3 values for each harbor follow the predicted trend of decreasing wave energy exposure from Manukau to Whangapoua, there is a high degree of overlap between sites in the different harbors for most of the site environmental characteristics shown in Table 2.

Sand-sized particles (i.e., 0.0625–2 mm diameter) accounted for between 91.57 and 99.15% of the sediment dry mass at all sites (Table 2). Most of the gravel-sized sediment particles (i.e., >2 mm diameter) found at these sites were shell fragments. Counts of adult *Macomona* made during preliminary plot excavations suggest a broad overlap in densities from the three harbors (Fig. 2). Among-site variation in the ambient density of adult *Macomona* was greatest at Manukau, the largest and most wave exposed harbor.

Although chlorophyll *a* concentrations tended to be slightly higher in ambient sediments (Fig. 3a), there was no significant difference in chlorophyll *a* in the zero-*Macomona* experimental plots (relative to outside the plots) across all sites 4 d after the experiment started (paired *t* test, df = 8, P = 0.103). In contrast, the mean depth of the apparent RPDZ was significantly less in the experimental plots than in the adjacent ambient sediment (paired *t* test, df = 8, P = 0.0132), although this difference over all sites was driven by conditions in Manukau (Fig. 3b). Very few dead *Macomona* were observed on the sediment surface of the experimental plots. Experimental plots had assumed an appearance identical to that of the surrounding sediment within one week of their creation.

Mean densities of adult *Macomona* retrieved from each treatment are shown in Fig. 4. While these densities differed from the initial transplant density, at each site treatments remained significantly different from one another (generalized linear model, Poisson errors, df = 16, P = 0.0001 for each site-dependent treatment comparison), indicating that we successfully maintained significantly different treatment densities of adult *Macomona* in our experiment.

Experimental results

Across all sites and harbors, only small juveniles of three infaunal bivalve species (i.e., *Macomona, Austrovenus,* and *Nucula*), and large juveniles of *Macomona* were sufficiently common to warrant statistical analysis of experimental effects, and to assess how those experimental effects were modified by wave climate. Juvenile bivalve densities varied considerably between harbors and sites within harbors (Fig. 5).

Analysis of the influence of experimental factors on the density of juvenile bivalves provides a clear indication that the results of our experiment were location-dependent (Table 3). Significant interactions between experimental treatment and harbors, and sites nested within harbors were apparent (Table 3). As the design and analysis of this experiment nested sites within harbors, we are not able to completely isolate the influence of sites and harbors. Differences between harbors and between sites within harbors were important factors influencing the density of each of the juvenile bivalve species. Comparing effects on small and large *Macomona* juveniles reveals that harbor, site within harbor, and the interaction terms were all more important for the small juveniles (Table 3).

We used the information on site dependent variation in wind-wave climate, over the course of the experiment, to explain variation in the strength of the inter-

TABLE 2. Environmental characteristics of three experimental sites in each of three harbors in New Zealand.

Harbor	Site	Immersion (% time site covered)	Largest wave (wave ht. [m]; wave period [s])†	Mean wave (wave ht. [m]; wave period [s])†	Total time waves present (%)	Time waves present when site immersed (%)
Manukau	1	41.5	0.2; 9	0.083; 1.66	22.7	54.6
	2	77.3	0.4; 9	0.164; 1.25	25.5	32.9
	3	63.7	0.3; 11	0.106; 2.50	46.1	72.4
Tauranga	1	72.8	0.2; 3	0.089; 1.03	8.2	11.3
	2	82.5	0.3; 9	0.047; 2.53	48.8	59.2
	3	81.4	0.3; 3	0.064; 0.94	26.0	31.9
Whangapoua	1	33.4	0.1; 10	0.027; 1.43	31.4	94.0
	2	48.9	0.2; 2	0.081; 0.96	4.9	10.0
	3	48.1	0.2; 4	0.052; 1.30	1.9	3.9

† Wave parameters are given as: wave height in meters; wave period in seconds.

action between adult *Macomona* and juvenile bivalves. Interaction strength was characterized by deriving slope estimates from site-specific generalized-linear models of adult *Macomona* with dependent variables of the density of small and large *Macomona* juveniles, and small juvenile *Austrovenus* and *Nucula* (Table 4). Differences in the experimental effects between sites are clearly illustrated by variations in the slope estimates presented in Table 4. While a number of models were investigated for each species/size class (see *Methods: Statistical analyses*), in all cases normal error structures with log transformation of adult densities were the most appropriate and, except for large juvenile *Macomona*, juvenile data were untransformed. A backwards selection procedure with an exit criterion of 0.15 was used. The environmental variables available from each site included surficial sediment grain size, ambient density of adult *Macomona*, and the variables derived from the DOBIE (Fig. 2, Table 2). To reduce the number of environmental variables used in the multiple regression, Pearson correlation coefficients were calculated between each of the variables to eliminate highly covarying parameters. This resulted in six environmental variables for use in the multiple regression (percentage sand, ambient density of adult *Macomona* found while excavating the plots, maximum U_b^3, average U_b^3, number of data bursts recording waves, and time waves present as a percentage of total time). Maximum U_b^3 and average U_b^3 were only weakly correlated, which is not surprising given the short duration of the wave record (35 d).

The most parsimonious models explaining the effect of the site environmental variables on experimental treatment effects are presented in Table 5. These regression models were very successful in explaining differences in the experimental treatment effects between sites, with a minimum of 66% and a maximum of 99% of the variance explained by the models. Information on wave climate over the duration of the experiment proved to be very useful; both average and maximum U_b^3 were important variables explaining location-de-

pendent treatment effects. These two aspects of the wave climate appeared to work in different ways, however. Average U_b^3 increased the negative effect of adult *Macomona* on both size classes of *Macomona* juveniles and *Austrovenus* juveniles and maximum U_b^3 decreased it. For *Nucula* juveniles, the models indicate that average and maximum U_b^3 were not significant variables ($P > 0.05$). The most important variable influencing the effect of experimental treatments on the density of *Nucula* recruits was the percentage time waves were present. The models also provide evidence that ambient density of adult *Macomona*, immersion time, and percentage sand increased the negative interactions between experimental additions of adult *Macomona* and small and large *Macomona* juveniles.

DISCUSSION

High densities of adult *Macomona* have a negative effect on juvenile bivalves over a range of sites with different wave climates. Our predictions that wind-waves would be an important factor accounting for variation in the interaction between adult *Macomona* and juvenile bivalves was strongly supported by this study. If our analysis had stopped after the identification of significant location treatment interactions, we could only have concluded that interactions between adult *Macomona* and juvenile bivalves were dependent on location. No indication of the broader-scale processes constraining adult–juvenile interactions could have been identified. The subsequent meta-analyses enabled us to identify that various aspects of the wave climate measured over the course of the experiment and the ambient density of adult *Macomona* surrounding the experimental plots were important factors influencing variations in experimental results from site to site. The importance of these factors could not have been investigated without designing our experiments to include variability between sites as information rather than treating it as random noise. Thus, this experiment successfully generalizes findings from earlier studies conducted at one location (Thrush et al. 1994,

Table 2. Extended.

Number of data bursts recording waves	Total U_b^3 (cm³/s³)	Average U_b^3 (cm³/s³)	Maximum U_b^3 (cm³/s³)	Maximum/ average U_b^3	Percentage gravel	Percentage sand	Percentage silt–clay
370	678 980	1 835	24 288	13.2	0.52	98.80	0.69
419	1 493 767	3 565	94 507	26.5	26.5	98.17	1.10
738	1 055 093	1 430	47 793	33.4	0.25	99.15	0.60
139	25 479	183	2 369	12.9	0.38	97.90	1.73
798	110 473	138	7 704	55.8	3.13	91.57	5.30
419	64 675	154	3 753	24.4	1.40	97.82	0.77
483	323 467	670	11 790	17.6	1.77	97.64	0.59
83	13 314	160	1 083	6.8	3.20	96.01	0.78
32	5 029	157	784	5.0	2.5	97.07	0.40

1996a, 1997b, Hewitt et al. 1996, 1997a, Turner et al. 1997).

The continuous measurement of the wave climate at each site over the course of the experiment enabled us to assess the role of the different wave-climate variables. Both the average and maximum U_b^3 were important variables influencing the relationships of juvenile bivalves with adult *Macomona* (Table 5, Fig. 6). Interestingly, average U_b^3 enhanced negative interactions between adult *Macomona* and juvenile bivalves, while maximum U_b^3 worked to weaken these negative relationships. Bell et al. (1997) demonstrated that on extensive intertidal sandflats, very small waves (6–8 cm high) are capable of entraining sediments (and presumably juvenile bivalves) when the water is shallow and tidal current velocities are high over the mid-tide sections of the shore. As average U_b^3 enhanced negative interactions, this probably increases the opportunity for juvenile bivalves to be resuspended and move away from locally unfavorable areas (e.g., high densities of adult *Macomona*). In contrast, maximum U_b^3 probably reflects the potential for physical processes to domi-
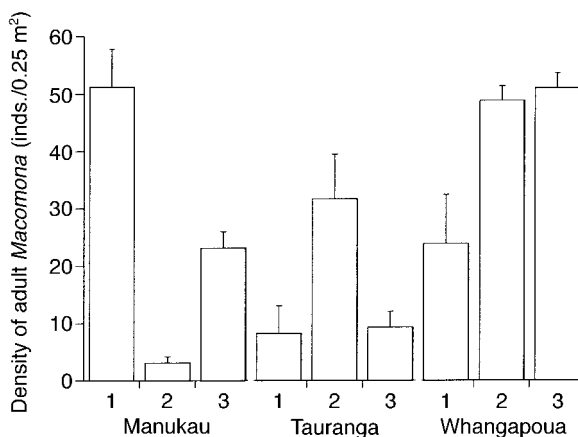

Fig. 2. Ambient density of adult *Macomona* (mean + 1 SD) recorded during excavation of experimental plots at the start of the experiment. Sites within harbors are represented by numbers 1–3.

nate, obscuring spatial patterns generated by local biotic interactions and thus decreasing the strength of experimental effects (Commito et al. 1995b, Turner et al. 1997). A high maximum U_b^3 probably reflects an event occurring during the experiment that obliterated any spatial pattern built up by adult–juvenile interactions. The amount of time over the experimental period that waves were present also had an important influence on the experimental effects for small juvenile *Macomona* and *Nucula* (Table 5). Thus the critical factor influencing the site to site variability in adult–juvenile interactions between *Macomona* and juvenile bivalves is the ratio of maximum to average event size (Table 2). Determining the details of such mechanisms will require intensive behavioral observations under conditions that reflect the natural dynamics of the environment (see Snelgrove and Butman 1994).

The other environmental variables did not have such consistent effects on the adult–juvenile interactions. Ambient density of adult *Macomona* in the vicinity of the experimental plots was an important factor influencing the strength of experimental effects for *Macomona* and *Nucula* juveniles, but not for *Austrovenus* juveniles (Table 5, Fig. 6). Ambient adult *Macomona* density can reflect the broader-scale suitability of sites to juveniles or act as a surrogate factor for processes operating on a broader scale than the experimental plot size (e.g., the role of predator density, food supply). Also, high ambient densities of adult *Macomona* surrounding the experimental plots may strengthen negative effects by effectively increasing the patch size of high density treatments. The role of ambient adult *Macomona* density identified in this experiment is consistent with an earlier intensive experiment conducted at site 1 in Manukau (Thrush et al. 1997a, b). Immersion time was only an important factor for *Macomona* juveniles, with sites lower on the shore tending to exhibit stronger experimental effects, probably as a result of increasing the length of time available for juvenile bivalves to move away from unsuitable areas. The nine sites used in this experiment encompassed sites that were immersed from ~33–82% of the time (Table 2).
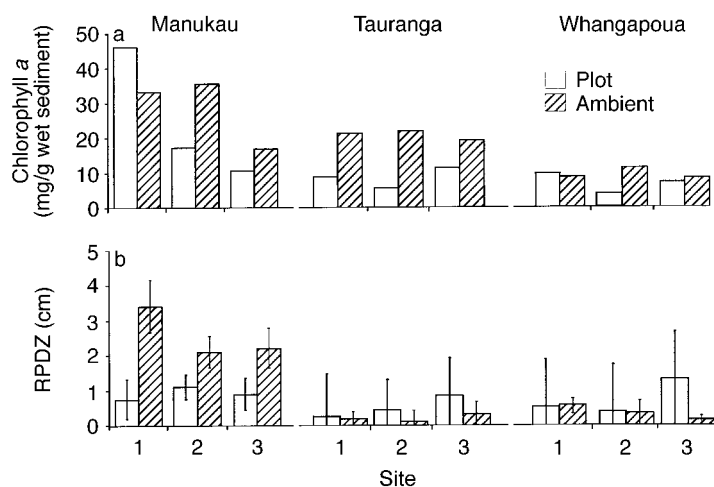
Fig. 3. (a) Surficial sediment chlorophyll *a* concentration and (b) mean (±1 SE) depth to the apparent redox potential discontinuity zone (RPDZ) in and out of the zero-*Macomona* addition experimental plots 4 d after the experiment started. Sites within harbors are represented by numbers 1–3.

The models for both the small and large *Macomona* juveniles also included percentage sand. However, differences in sand content between sites were small (Table 2) and did not make a major contribution to variation in the adult–juvenile interactions (Table 5).

Differences in the strength of the negative relationship between specific juvenile bivalves (species and size classes) and adult *Macomona* expected at the different sites can be demonstrated as a result of the meta-analysis. We can identify whether the site environmental variables should operate to strengthen, weaken or have little effect on the adult–juvenile relationship at each site by examining Tables 2 and 5, and Fig. 2. Tallying up the factors that work to strengthen or weaken the negative effects of adult *Macomona* on small juvenile conspecifics, the sites with the weakest negative effects were site 1 in Whangapoua and site 3 in Tauranga. Whangapoua site 1 had no factors strengthening the adult–juvenile interaction: immersion time was short and average U_b^3 and ambient adult *Macomona* densities were low. Tauranga site 3 had a high immersion time, which should strengthen negative effects, but low ambient densities of adult *Macomona* and low average U_b^3 which would work against an effect

being observed. All of the sites in Tauranga had both low ambient densities of adult *Macomona* and low average U_b^3, although these factors would to some extent be offset by high immersion times and the low maximum U_b^3. In Manukau Harbour, sites 1 and 3 had more factors working to strengthen adult–juvenile interactions than weaken them. Site 1 exhibited the highest ambient density of *Macomona,* a high average U_b^3, a high sand content and a low immersion time. Site 3 also had a high average U_b^3 and high sand content, but had low ambient densities of adult *Macomona.* Our ability to demonstrate an adult–juvenile relationship at each site was altered as the *Macomona* grew into the next size class (i.e., small vs. large juvenile *Macomona,* Table 5). The influence of immersion time weakened and the influence of the percent time waves were recorded at the site disappeared. For large juvenile *Macomona,* the sites least likely to support negative effects of adults were site 2 in Tauranga and site 1 in Whangapoua. Site 1 in Manukau was still the site at which most of the environmental factors worked to strengthen negative relationships with large juvenile *Macomona,* however, effects were more pronounced at site 3.

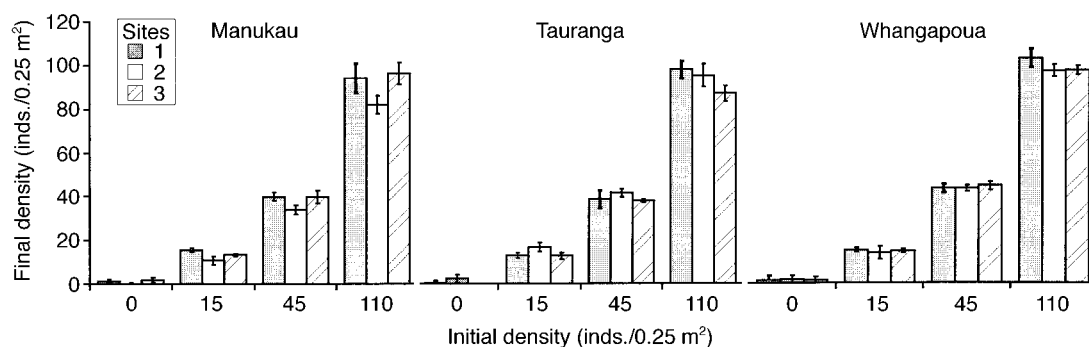An earlier study by Legendre et al. (1997) demon-

Fig. 4. Density of adult *Macomona* (mean ± 1 SE) recorded in the experimental plots at the end of the experiment.
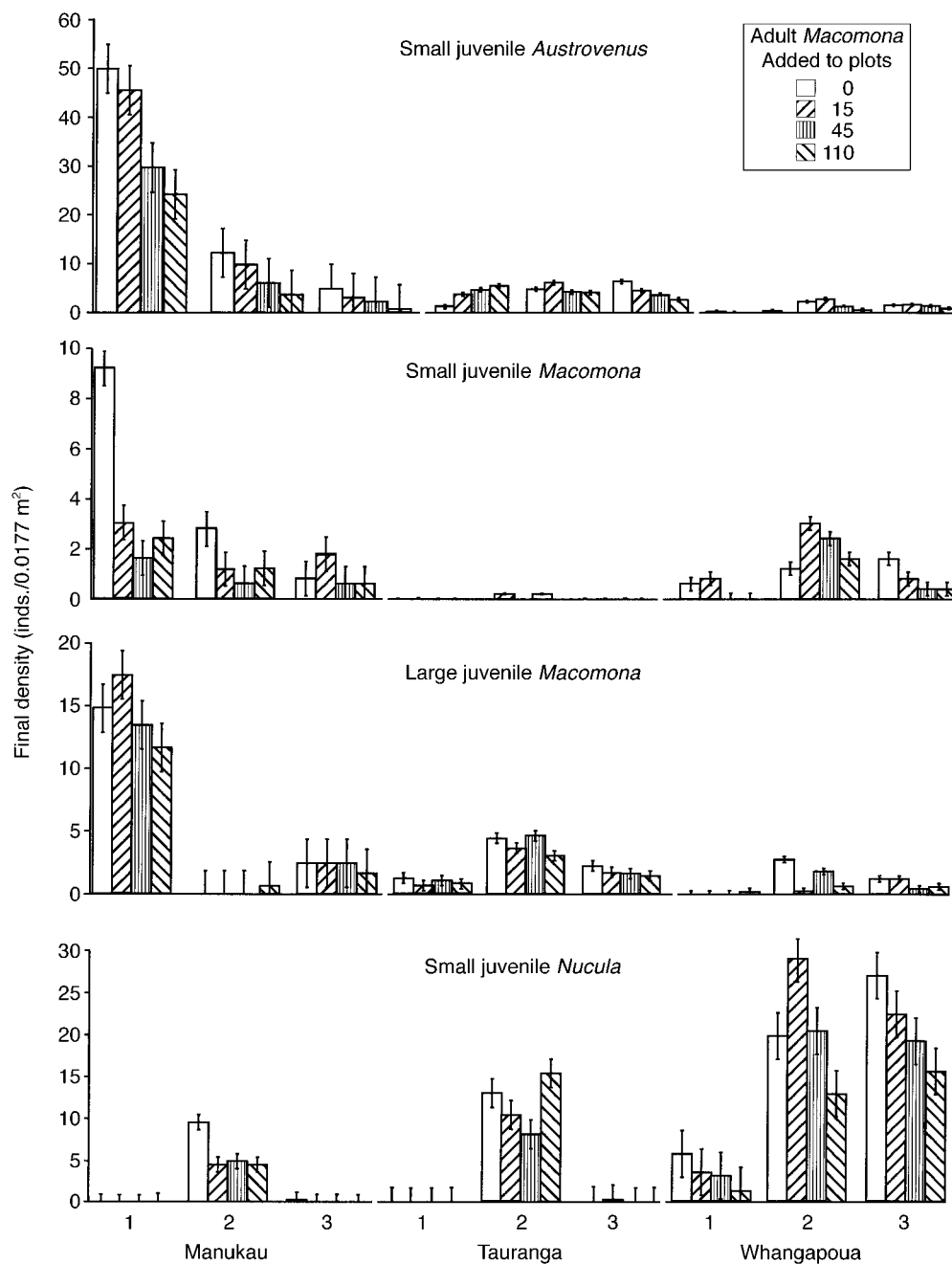
FIG. 5. Density of juvenile bivalves (mean ± 1 SE) recorded from each treatment at each site in each harbor at the end of the experiment. For each site, blocks are ordered from left to right from the 0, 15, 45, 110 adult *Macomona* addition plots.

strated the utility of predicted wave-disturbance gradients running up the shore in accounting for the distribution of juvenile bivalves. However, a simple ranking of the sites in our study, based on the typical wind velocity of each harbor and the relative exposure of individual sites, would not have proved as informative as direct measurement of the wave climate. One reason for this is that during the course of this experiment winds blew from the northeast, whereas typically winds

blow from the southwest. Another reason is that our study was conducted across one habitat type and in this context waves are a dynamic variable; they do not simply force changes in beach morphology or reflect gradients of physical habitat disturbance. A third reason is that the empirical models developed provide some insight into how local ecological interactions are modified by processes operating over broader spatial scales. For the range exhibited by the environmental variables

TABLE 3. The significance of experiment, harbor, site within-harbor, and interaction effects on the density of juvenile bivalves determined by generalized linear models.

A) Small juvenile *Macomona*
Model type: negative binomial errors, log-link, Pearson χ^2, df = 0.94

Effect	df	χ^2	P
Harbor	2	83.77	0.0001
Experiment	1	2.82	0.0931
Site(Harbor)	6	90.17	0.0001
Experiment × Harbor	2	5.44	0.0659
Experiment × Site(Harbor)	6	13.11	0.0414

B) Large juvenile *Macomona*
Model type: normal errors, log-link, error MS = 9.57, df = 162

Effect	df	MS	F	P
Harbor	2	236.77	24.75	0.0001
Experiment	1	64.51	6.75	0.0103
Site(Harbor)	6	14.06	1.47	0.1916
Experiment × Harbor	2	23.77	2.48	0.0866
Experiment × Site(Harbor)	6	2.47	0.26	0.9553

C) Small juvenile *Austrovenus*
Model type: negative binomial errors, log-link, Pearson χ^2, df = 0.94

Effect	df	χ^2	P
Harbor	2	25.02	0.0001
Experiment	1	5.36	0.0206
Site(Harbor)	6	188.64	0.0001
Experiment × Harbor	2	8.80	0.0123
Experiment × Site(Harbor)	6	15.44	0.0171

D) Small juvenile *Nucula*
Model type: normal errors, log-link, error MS = 160, df = 40.79

Effect	df	MS	F	P
Harbor	2	2473.18	60.64	0.0001
Experiment	1	254.32	6.24	0.0135
Site(Harbor)	6	644.51	15.80	0.0001
Experiment × Harbor	2	273.30	6.70	0.0016
Experiment × Site(Harbor)	6	40.53	0.99	0.4315

we measured, Tables 4 and 5 can be used to quantify the effect of wave climate variables on the slope of the negative relationships between adult *Macomona* and juvenile bivalves. For example, when everything else

is constant, increasing the average U_b^3 by 100 cm³/s³ is predicted to increase the slope of the negative relationship for small juvenile *Macomona* by 0.5, i.e., about 18% at site 1 in Manukau.

It is interesting to consider the possible broader ecological implications of interactions between wind-waves and adult–juvenile interactions, even though extrapolating beyond the range of the variables used in the model is risky. As the size and location of individuals within the sediment change with age, the relative importance of ''extreme'' vs. ''average'' conditions will vary. For example, as juvenile *Macomona* grow beyond 1 cm they are found less frequently in the water column, which restricts their potential for dispersal from unfavorable areas. Also as *Macomona* grow they live deeper in the sediment, thus increasing the size of the extreme wave event that is needed to resuspend and move the bivalves. This decreased mobility with age generates spatial relationships dependent on age/size (Hewitt et al. 1996) and enhances separation of age classes along physical gradients (Legendre et al. 1997). Macrofaunal species with different modes of living within the sediment will have different potentials to be moved by waves (Tamaki 1987). A combination of behavior and resistivity to transport by waves can result in species-dependent differences in the persistence of spatial relationships (Hewitt et al. 1997*b*). High densities of organisms that bind the sediment and modify wave-induced erosion potential can also mitigate wave disturbance effects on other infauna (Thrush et al. 1996*b*). The role of extreme and average waves in soft-sediment habitats contrasts with studies of organisms that encrust rocky shores, where extreme waves appear to be the dominant factor in the wave climate (Denny 1995). Wave climates can modify sediment grain size, food supply, and beach profile and thus define differences between habitats. While dynamic hydrodynamic factors can have important influences on benthic community structure (Warwick and Uncles 1980, Warwick et al. 1991), we do not yet understand

TABLE 4. Site-specific regressions used to derive slope estimates to assess the role of environmental factors in influencing the strength of experimental effects.

Harbor	Site	Small juvenile *Macomona*			Large juvenile *Macomona*†			Small juvenile *Austrovenus*			Small juvenile *Nucula*		
		Slope	r^2	P	Slope	r^2	P	Slope	r^2	P	Slope	r^2	P
Manukau	1	−5.771	0.19	0.035	−1.168	0.277	0.0337	−1.046	0.035	0.433	0		
	2	−0.542	0.02	0.261	−0.269	0.082	0.2197	0.028	0.062	0.2972	−0.534	0.412	0.002
	3	−0.633	0.12	0.080	−0.146	0.085	0.767	−0.178	0.043	0.3817	−0.062	0.226	0.034
Tauranga	1	−0.305	0.03	0.218	0			−0.010	0.001	0.9082	0.003	0.003	0.828
	2	−0.566	0.07	0.145	0.121	0.032	0.5326	0.079	0.008	0.7168	0.566	0.013	0.627
	3	0.530	0.05	0.184	0			−0.035	0.029	0.4739	0		
Whanga-poua	1	0.015	0.04	0.678	−0.142	0.020	0.5529	0.015	0.035	0.4325	−0.156	0.028	0.484
	2	−0.375	0.13	0.072	−0.257	0.030	0.464	−0.192	0.129	0.131	−1.512	0.126	0.124
	3	−0.081	−0.04	0.595	−0.485	0.156	0.0509	−0.002	0.005	0.9791	−0.962	0.100	0.173

Note: Experimental additions of adult *Macomona* were log transformed in all cases.
† Regressions based on log transformed juvenile count data.

TABLE 5. Multiple regression models identifying the influence of site-dependent environmental factors on the experimental effects.

Species [transformation]	r^2_{adj}	Factor	Parameter estimate	P
Small juvenile *Macomona* [semi-log]	0.98	Average U_b^3	−0.00455600	0.0188
		Maximum U_b^3	0.00016643	0.0212
		Immersion time	−0.10869238	0.0305
		Ambient adult *Macomona* density	−0.08861184	0.0349
		Percentage sand	−0.48967243	0.0531
		Percentage time waves present	−0.02517098	0.0686
Large juvenile *Macomona* [log–log]	0.99	Percentage sand	−0.06288972	0.0205
		Average U_b^3	−0.00066	0.0039
		Maximum U_b^3	0.000021	0.0069
		Ambient adult *Macomona* density	−0.01434311	0.0055
		Immersion time	−0.00534759	0.0840
Small juvenile *Austrovenus* [semi-log]	0.66	Average U_b^3	−0.00081523	0.0142
		Maximum U_b^3	0.00002900	0.0178
Small juvenile *Nucula* [semi-log]	0.97	Percentage time waves present	0.002100	0.0178
		Ambient adult *Macomona* density	−0.017700	0.0696
		Maximum U_b^3	−0.000039	0.0862
		Average U_b^3	0.008100	0.1270

the role of these processes in community function in soft-sediment ecosystems. In our study, we are limited in drawing conclusions about the biological significance of the different wave parameters because of the difficulty of collecting a time series of bivalve responses to match the time series of wave data. Collecting data on dynamic physical processes from a number of study sites, and relating this information to ecological responses that are sampled at much lower frequencies, is an important problem when trying to address the interaction between local ecological processes and broader-scale dynamic physical variables.

Problems have arisen in population and community ecology when the results of studies conducted at one or a few locations have been extrapolated to develop general theory. Subsequent studies have often failed to support the generalizations from earlier studies (e.g., Wiens 1976, Dayton 1984, Dayton and Tegner 1984*a,* Underwood and Denley 1984, Foster 1990, Menge 1991, Dayton 1994, Brown 1995, Beck 1997). Essentially, this is a problem with the scale dependence of ecological processes. As detailed studies of local ecological processes have been conducted over a greater range of locations in space and time, we see more and more that other factors operating over broader scales constrain the outcome of local ecological processes. This implies that generality in the results and conclusions of experimental studies can only be gained by conducting studies at a variety of locations; generality is gained by increasing the extent of a study over a broader range of conditions. Nesting experiments at a few locations within a broader base of information gathered by surveying is an efficient way of inferring the generality of experiments (Menge et al. 1997*a,* Thrush et al. 1997). Simply describing the role of processes operating over broad scales may not increase the predictive power of population and community

ecology; formal statistical analyses may be necessary. Understanding the natural history is also important, especially when the variability in ecological structure and function can be ascribed to small-scale processes. Careful consideration of the balance between gaining more detailed information vs. more general information is always necessary.

One solution to the problem of identifying the generality of local ecological processes is to randomly choose experimental sites (Beck 1997). This procedure requires an adequate level of replication of study sites to provide an unbiased estimate of the potential range of effects over the statistical population of study sites (Eberhardt and Thomas 1991, McKone and Lively 1993). However, variability may not be randomly distributed in space and time (e.g., Haury 1978, Hassell et al. 1991, Steele 1991, Thrush 1991, He and Legendre 1996, Hewitt et al. 1996). If variance in ecological variables is not random (i.e., white noise) but increases with spatial and temporal scale (i.e., red shifted), then higher and higher levels of replication will be necessary to control for increasing variation (Schneider 1994). This would make it even less likely that random allocation of experimental sites can provide a cost effective solution to increasing the generality of field experiments. A cost/benefit comparison of the different approaches to increasing the generality of field experiments has yet to be conducted. However, unless the appropriate covariables are measured, random allocation of multiple sites can provide an indication of how local ecological processes vary from place to place, but not why they vary.

We suggest that while increasing the spatial extent of a study is likely to increase the physical and biological heterogeneity encompassed, understanding how these change the results of local processes is necessary. Assessing the generality of the role particular processes
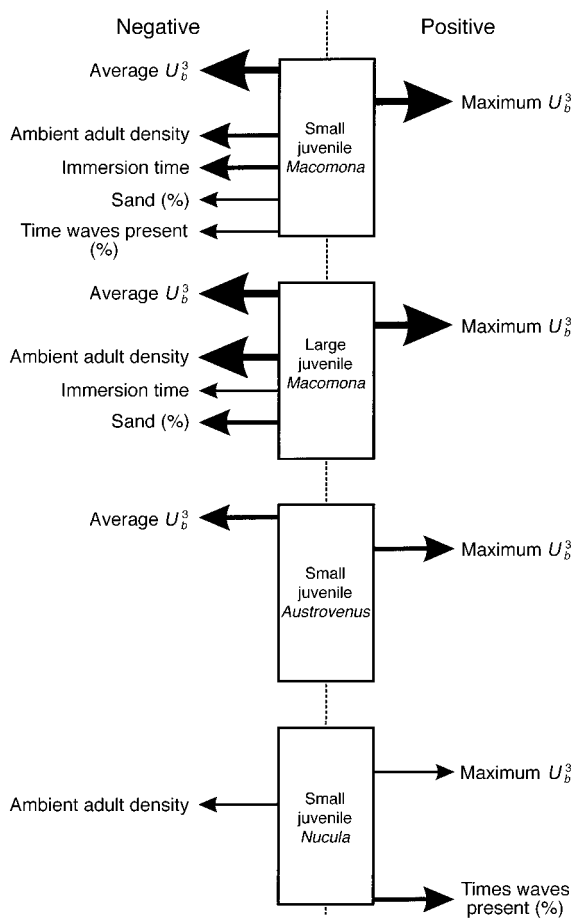
FIG. 6. The influence of environmental factors on the density-dependent interaction between adult *Macomona* and juvenile bivalves. Factors increasing the strength of negative interactions are shown on the left of the diagram, while factors on the right-hand side of the diagram decrease the strength of negative effects. The size of the arrows indicates the strength of the effect of the variable on the interaction as indicated by the P values presented in Table 5 (large arrows, $P < 0.01$; medium arrows, $0.01 > P < 0.05$; small arrows, $0.05 > P < 0.15$).

play in influencing the structure and function of populations and communities is a question of scale. In this study we made a priori predictions about the importance of variables that we thought were likely to influence the outcome of adult–juvenile interactions from sandflat to sandflat. We performed our experiment across a series of sandflats, encompassing a range of conditions, and measured what we predicted to be the key variables constraining the local interaction within one habitat. The use of meta-analysis to assess the role of the dynamic wave climate and other environmental site variables in influencing the strength of local adult–juvenile interactions provided a cost-effective way of increasing the generality of the experiment and improving our understanding of how local interactions are modified by broader-scale processes. This approach

is another way of linking large-scale information to small-scale studies that identify mechanisms, by nesting experiments within larger scale patterns (Schneider 1978, Wiens 1989, Menge et al. 1994, Menge et al. 1997*a*, Thrush et al. 1997*a*).

LITERATURE CITED

Ahn, I. Y., G. Lopez, and R. Malouf. 1993. Effects of the gem clam *Gemma gemma* on the early post-settlement emigration, growth and survival of the hard clam *Merceneria merceneria*. Marine Ecology Progress Series **99**:61–70.

Andre, C., P. R. Jonsson, and M. Lindegarth. 1993. Predation on settling bivalves by benthic suspension feeders: the role of hydrodynamics and behaviour. Marine Ecology Progress Series **97**:183–192.

Armonies, W. 1992. Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. Marine Ecology Progress Series **83**:197–206.

Beck, M. W. 1997. Inference and generality in ecology: current problems and an experimental solution. Oikos **78**:265–273.

Bell, R. G., T. M. Hume, T. J. Dolphin, M. O. Green, and R. A. Walters. 1997. Characterisation of physical factors on an intertidal sandflat, Manukau Harbour, New Zealand. Journal of Experimental Marine Biology and Ecology **216**: 11–32.

Beukema, J. J., and J. de Vlas. 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. Marine Ecology Progress Series **52**:193–200.

Bock, M. J., and D. C. Miller. 1995. Storm effects on particulate food resources on an intertidal sandflat. Journal of Experimental Marine Biology and Ecology **187**:81–101.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago, Illinois, USA.

Butman, C. A. 1987. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrological processes. Oceanography and Marine Biology: an Annual Review **25**:113–165.

Butman, C. A., J. P. Grassle, and C. M. Webb. 1988. Substrate choices made by marine larvae settling in still water and flume flow. Nature **333**:771–773.

Commito, J. A., C. A. Currier, L. R. Kane, K. A. Reinsel, and I. M. Ulm. 1995*a*. Dispersal dynamics of the bivalve *Gemma gemma* in a patchy environment. Ecological Monographs **65**:1–20.

Commito, J. A., S. F. Thrush, R. D. Pridmore, J. E. Hewitt, and V. J. Cummings. 1995*b*. Dispersal dynamics in a wind-driven benthic system. Limnology and Oceanography **40**: 1513–1518.

Crawley, M. J. 1993. GLIM for ecologists. Blackwell Scientific, Oxford, UK.

Cummings, V. J., R. D. Pridmore, S. F. Thrush, and J. E. Hewitt. 1996. Effect of the spionid polychaete *Boccardia syrtis* on the distribution and survival of juvenile *Macomona liliana* (Bivalvia: Tellinacea). Marine Biology **126**: 91–98.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization

of space in a rocky intertidal community. Ecological Monographs **41**:351–389.

Dayton, P. K. 1984. Processes structuring some marine communities: are they general? Pages 181–200 *in* J. D. R. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle, editors. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, USA.

Dayton, P. K. 1994. Community landscape: scale and stability in hard bottom marine communities. Pages 289–332 *in* A. G. Hildrew, P. S. Giller, and D. Raffaelli, editors. Aquatic ecology: scale, pattern and processes. Blackwell Scientific, Oxford, UK.

Dayton, P. K., and J. S. Oliver. 1977. Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. Science **197**:55–58.

Dayton, P. K., G. A. Robillard, and R. T. Paine. 1970. Benthic faunal zonation as a result of anchor ice formation in McMurdo Sound, Antarctica. Pages 244–258 *in* M. W. Holdgate, editor. Antarctic ecology. Academic Press, London, UK.

Dayton, P. K., and M. J. Tegner. 1984a. The importance of scale in community ecology: a kelp forest example with terrestrial analogs. Pages 457–483 *in* P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, editors. A new ecology: novel approaches to interactive systems. John Wiley and Sons, New York, New York, USA.

Dayton, P. K., and M. J. Tegner. 1984b. Catastrophic storms, El Nino, and patch stability in a Southern California kelp community. Science **224**:283–285.

Delgado, M., V. N. de Jonge, and H. Peletier. 1991. Experiments on resuspension of natural microphytobenthos populations. Marine Biology **108**:321–328.

Denny, M. 1995. Predicting physical disturbance: mechanistic approaches to the study of survivorship on wave-swept shores. Ecological Monographs **65**:371–418.

Dobbs, F. C., and Vozarik. 1983. Immediate effects of a storm on coastal infauna. Marine Ecology Progress Series **11**:273–279.

Dolphin, T. J., T. M. Hume, and K. E. Parnell. 1995. Sedimentary and oceanographic processes on a sandflat in an enclosed sea, Manukau Harbour, New Zealand. Marine Geology **128**:169–181.

Eberhardt, L. L., and J. M. Thomas. 1991. Designing environmental field studies. Ecological Monographs **61**:53–73.

Eckman, J. E. 1979. Small-scale patterns and processes in a soft substratum intertidal community. Journal of Marine Research **37**:437–457.

Emerson, C. W. 1989. Wind stress limitation of benthic secondary production in shallow, soft-sediment communities. Marine Ecology Progress Series **53**:65–77.

Emerson, C. W., and J. Grant. 1992. The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. Limnology and Oceanography **36**:1288–1300.

Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecological Monographs **65**:75–100.

Foster, M. S. 1990. Organisation of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. Hydrobiologia **192**:21–33.

Giller, P. S., A. G. Hildrew, and D. Raffaelli. 1994. Aquatic ecology: scale, pattern and process. Blackwell Scientific, Oxford, UK.

Grant, J. 1985. A method for measuring horizontal transport of organic carbon over sediments. Canadian Journal of Fisheries and Aquatic Sciences **42**:595–602.

Gurevitch, J., and L. V. Hedges. 1993. Meta-analysis: combining the results of independent experiments. Pages 378–398 *in* S. M. Scheiner and J. Gurevitch, editors. Design

and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.

Hairston, S. N. G. 1989. Ecological experiments: purpose, design and execution. Cambridge University Press, Cambridge, UK.

Hassell, M. P., H. N. Comins, and R. M. May. 1991. Spatial structure and chaos in insect population dynamics. Nature **353**:255–258.

Haury, L. R. 1978. Patterns and processes in the time-scales of plankton distributions. Pages 277–327 *in* J. Steele, editor. Spatial pattern in plankton communities. Plenum Press, New York, New York, USA.

He, F. L., and P. Legendre. 1996. On species–area relations. American Naturalist **148**:719–737.

Hewitt, J. E., P. Legendre, B. H. McArdle, S. F. Thrush, C. Bellehumeur, and S. M. Lawrie. 1997a. Identifying relationships between adult and juvenile bivalves at different spatial scales. Journal of Experimental Marine Biology and Ecology **216**:77–98.

Hewitt, J. E., R. D. Pridmore, S. F. Thrush, and V. J. Cummings. 1997b. Assessing the short-term stability of spatial patterns of macrobenthos in a dynamic estuarine system. Limnology and Oceanography **42**:282–288.

Hewitt, J. E., S. F. Thrush, V. J. Cummings, and R. D. Pridmore. 1996. Matching patterns with processes: predicting the effect of size and mobility on the spatial distributions of the bivalves *Macomona liliana* and *Austrovenus stutchburyi*. Marine Ecology Progress Series **135**:57–67.

Hines, A. H., M. H. Posey, and P. J. Haddon. 1989. Effects of adult suspension- and deposit-feeding bivalves on recruitment of estuarine infauna. Veliger **32**:109–119.

Hume, T. M., and C. E. Herdendorf. 1993. On the use of empirical stability relationships for characterising estuaries. Journal of Coastal Research **9**:413–422.

Kareiva, P., and M. Andersen. 1988. Spatial aspects of species interactions: the wedding of models and experiments. Pages 38–54 *in* A. Hastings, editor. Community ecology, lecture notes in biomathematics. Springer-Verlag, New York, New York, USA.

Keddy, P. A. 1991. Working with heterogeneity: an operator's guide to environmental gradients. Pages 181–201 *in* J. Kolasa and S. T. A. Pickett, editors. Ecological heterogeneity. Springer-Verlag, New York, New York, USA.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology **74**:1659–1673.

Legendre, P., S. F. Thrush, V. J. Cummings, P. K. Dayton, J. Grant, J. E. Hewitt, A. H. Hines, B. H. McArdle, R. D. Pridmore, D. C. Schneider, S. J. Turner, R. B. Whitlatch, and M. R. Wilkinson. 1997. Spatial structure of bivalves in a sandflat: scale and generating processes. Journal of Experimental Marine Biology and Ecology **216**:99–128.

Levin, S. A. 1988. Pattern, scale and variability: an ecological perspective. Pages 1–12 *in* A. Hastings, editor. Community ecology. Springer-Verlag, Berlin, Germany.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943–1967.

Longuet-Higgins, M. S. 1952. On the statistical distribution of the heights of sea waves. Journal of Marine Research **11**:245–266.

Longuet-Higgins, M. S. 1975. On the joint distribution of the periods and amplitudes of sea waves. Journal of Geophysical Research **80**:2688–2694.

Madsen, O. S. 1976. Wave climate of the continental margin: elements of its mathematical description. Pages 65–87 *in* D. J. Stanley and D. J. P. Swift, editors. Marine sediment transport and environmental management. John Wiley and Sons, New York, New York, USA.

McCullagh, P., and J. A. Nelder. 1989. Generalised linear models. Chapman and Hall, London, UK.

McKone, M. J., and C. M. Lively. 1993. Statistical analysis

of experiments conducted at multiple sites. Oikos **67**:184–186.

Menge, B. A. 1976. Relative importance of recruitment and other causes of variation on rocky intertidal community structure. Journal of Experimental Marine Biology and Ecology **146**:69–100.

Menge, B. A. 1991. Generalizing from experiments: is predation strong or weak in the New England rocky intertidal? Oecologia **88**:1–8.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecological Monographs **65**:21–74.

Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: variations in interaction strength in a rocky intertidal habitat. Ecological Monographs **64**:249–286.

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997*a*. Benthic–pelagic links and rocky intertidal communities: bottom-up effects on top-down control? Proceedings of the National Academy of Sciences (USA) **94**:14 530–14 535.

Menge, B. A., B. A. Daley, P. A. Wheeler, and P. T. Strub. 1997*b*. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. Limnology and Oceanography **42**:57–66.

Miller, D. C. 1989. Abrasion effects in sandy sediments. Marine Ecology Progress Series **55**:73–82.

Miller, D. C., P. A. Jumars, and A. R. M. Nowell. 1984. Effects of sediment transport on deposit feeding: scaling arguments. Limnology and Oceanography **29**:1202–1217.

Nielsen, P. 1992. Coastal bottom boundary layers and sediment transport. World Scientific, Singapore.

Olafsson, E. B., C. H. Peterson, and W. G. J. Ambrose. 1994. Does recruitment limitation structure populations and communities of macroinvertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. Oceanography and Marine Biology Annual Review **32**:65–109.

O'Riordan, C. A., S. G. Monismith, and J. R. Koseff. 1995. The effect of bivalve excurrent jet dynamics on mass transfer in a benthic boundary layer. Limnology and Oceanography **40**:330–344.

Posey, M., W. Lindberg, T. Alphin, and F. Vose. 1996. Influence of storm disturbance on an offshore benthic community. Bulletin of Marine Science **59**:523–529.

Pridmore, R. D., S. F. Thrush, R. J. Wilcock, T. J. Smith, J. E. Hewitt, and V. J. Cummings. 1991. Effect of the organochlorine pesticide technical chlordane on the population structure of suspension and deposit feeding bivalves. Marine Ecology Progress Series **76**:261–271.

Rees, E. I. S., A. Nicholaidou, and P. Laskaridou. 1977. The effects of storms on the dynamics of shallow water benthic associations. Pages 465–476 *in* B. F. Keegan, P. O. O'Ceidigh, and P. J. S. Boaden, editors. Eleventh European marine biology symposium ''Biology of benthic organisms''. Pergamon, Oxford, UK.

Rosenthal, R. 1991. Meta-analytic procedures for social research. Sage Publications, Newbury Park, California, USA.

Roughgarden, J., S. D. Gaines, and S. W. Pacala. 1987. Supply side ecology: the role of physical transport processes. Pages 459–486 *in* P. Giller and J. Gee, editors. Organization of communities past and present. Blackwell Scientific, Oxford, UK.

Sartory, D. P. 1982. Spectrophotometric analysis of chlorophyll *a* in freshwater phytoplankton. Hydrological Research Institute Technical Report TR 115, Pretoria, South Africa.

SAS Institute. 1993. Technical report. SAS/statistical software: the GENMOD procedure. SAS Institute, Cary, North Carolina, USA.

SAS/Insight. 1993. Users' guide. Version six. SAS Institute, Cary, North Carolina, USA.

Schneider, D. C. 1978. Equalisation of prey numbers of migratory shorebirds. Nature **271**:353–354.

Schneider, D. C. 1992. Statistical evaluation of models in oceanography: analysis of Schaefer's trophic dynamic equation, rather than a surrogate. Limnology and Oceanography **37**:1076–1081.

Schneider, D. C. 1994. Quantitative ecology: spatial and temporal scaling. Academic Press, San Diego, California, USA.

Schneider, D. C., R. Walters, S. F. Thrush, and P. K. Dayton. 1997. Scale-up of ecological experiments: density variation in the mobile bivalve *Macomona liliana* Iredale. Journal of Experimental Marine Biology and Ecology **216**:129–152.

Snelgrove, P. V. R., and C. A. Butman. 1994. Animal–sediment relationships revisited: cause versus effect. Oceanography and Marine Biology Annual Review **32**:111–177.

Steele, J. H. 1991. Marine ecosystem dynamics: comparison of scales. Ecological Research **6**:175–183.

Tamaki, A. 1987. Comparison of resistivity to transport by wave action in several polychaete species on an intertidal sand flat. Marine Ecology Progress Series **37**:181–189.

Tegner, M. J., P. K. Dayton, P. B. Edwards, and K. L. Riser. 1997. Large-scale, low-frequency oceanographic effects on kelp forest succession: a tale of two cohorts. Marine Ecology Progress Series **146**:117–134.

Thrush, S. F. 1991. Spatial patterns in soft-bottom communities. Trends in Ecology and Evolution **6**:75–79.

Thrush, S. F., et al. 1997*b*. Matching the outcome of small-scale density manipulation experiments with larger scale patterns: an example of bivalve adult–juvenile interactions. Journal of Experimental Marine Biology and Ecology **216**: 153–170.

Thrush, S. F., J. E. Hewitt, R. D. Pridmore, and V. J. Cummings. 1996*a*. Adult–juvenile interactions of infaunal bivalves: contrasting outcomes in different habitats. Marine Ecology Progress Series **132**:83–92.

Thrush, S. F., R. D. Pridmore, J. E. Hewitt, and V. J. Cummings. 1994. The importance of predators on a sandflat: interplay between seasonal changes in prey densities and predator effects. Marine Ecology Progress Series **107**:211–222.

Thrush, S. F., D. C. Schneider, P. Legendre, R. B. Whitlatch, P. K. Dayton, J. E. Hewitt, A. H. Hines, V. J. Cummings, S. M. Lawrie, J. Grant, R. D. Pridmore, and S. J. Turner. 1997*a*. Scaling-up from experiments to complex ecological systems: where to next? Journal of Experimental Marine Biology and Ecology **216**:243–254.

Thrush, S. F., R. B. Whitlatch, R. D. Pridmore, J. E. Hewitt, V. J. Cummings, and M. Maskery. 1996*b*. Scale-dependent recolonization: the role of sediment stability in a dynamic sandflat habitat. Ecology **77**:2472–2487.

Turner, E. J., and D. C. Miller. 1991. Behaviour and growth of *Mercenaria mercenaria* during simulated storm events. Marine Biology **111**:55–64.

Turner, S. J., J. Grant, R. D. Pridmore, J. E. Hewitt, M. R. Wilkinson, T. M. Hume, and D. Morrisey. 1997. Bedload and water-column transport and colonization processes by mobile post-settlement benthic macrofauna: does infaunal density matter? Journal of Experimental Marine Biology and Ecology **216**:51–76.

Underwood, A. J., and E. J. Denley. 1984. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151–180 *in* J. D. R. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle, editors. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, USA.

Underwood, A. J., E. J. Denley, and M. J. Moran. 1983. Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. Oecologia **56**:202–219.

Warwick, R. M., J. D. Goss-Custard, R. Kirby, C. L. George, N. D. Pope, and A. A. Rowden. 1991. Static and dynamic environmental factors determining the community structure of estuarine macrobenthos in SW Britain: why is the Severn Estuary different? Journal of Applied Ecology **28**:329–345.

Warwick, R. M., and R. J. Uncles. 1980. Distribution of benthic macrofaunal associations in the Bristol Channel in relation to tidal stress. Marine Ecology Progress Series **3**: 97–103.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics **7**:81–120.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology **3**:385–397.

Woodin, S. A. 1976. Adult–larval interactions in dense faunal assemblages: patterns of abundance. Journal of Marine Research **34**:25–41.