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The sandflat habitat: scaling from experiments to conclusions

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1. Introduction

Ecological systems are characterised by spatial and temporal variations in the density of organisms and resources, and in the intensity of processes which affect them (e.g. Watt, 1947; Dayton, 1971; Addicot et al., 1987; Kolasa and Pickett, 1991; Giller et al., 1994). This heterogeneity represents both a difficulty for field study design and statistical testing, and a challenge to describe the spatial structuring of populations, communities and ecosystems (Legendre, 1993). Patterns in ecological and environmental variables are fundamental to developing hypotheses and in designing subsequent field studies, because they determine the spatial and temporal scales of study. Spatial and/or temporal patterns also provide useful stepping stones for addressing issues of scale. Patterns apparent at one scale can collapse to noise when viewed from other scales, indicating that patterns, processes and our perceptions vary in a scale-dependent manner. Perhaps the most important but rarely discussed issue is the question of how to scale-up

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from small-scale surveys and experiments to conclusions relevant at larger spatial and temporal scales.

It is useful to consider three separate components of scale: *grain*, the area of an individual sample (e.g. in surveys, core or quadrat; in experiments, replicate plot size); *lag*, the inter-sample distance; and *extent*, the total area over which samples were collected. While these descriptions originate from the geostatistical literature (see Isaaks and Srivastava, 1989), they have been applied to ecological studies (Wiens, 1989; Kotliar and Wiens, 1990; He et al., 1995). Comparisons of these various components provide an explicit description of the scope of an experiment or survey (Schneider, 1994). The appropriateness of a particular measurement scale will depend on the questions asked and the natural history characteristics of the organisms studied.

While patterns can be evaluated by surveying and used as a basis for generating hypotheses about mechanisms, experimental manipulations are usually (but not exclusively) used to test these hypotheses. Manipulations using controls and replicates are necessarily conducted at limited spatial and temporal scales (Levin, 1988; Hairston, 1989; Eberhardt and Thomas, 1991). However, many important ecological questions and pressing environmental problems concern integration over a wide range of spatial and temporal scales—especially the larger ones (Livingston, 1991; Carpenter et al., 1995; Thrush et al., 1995). Even where processes are operating on scales amenable to experimental manipulation, individual experiments frequently are conducted at only one location and the results of similar experiments in different locations are not always consistent (Thrush et al., 1996). Interpolating the results of studies by either extending the size of the area in which phenomena operate (i.e. changing the spatial grain) or generalising the results to different locations (i.e. changing the spatial extent) are important limitations currently facing ecologists, particularly in relating ecological changes to human impacts that are diffuse and/or operate over large spatial and temporal scales.

2. The workshop

In 1994 the National Institute of Water and Atmospheric Research (NIWA) sponsored a workshop to examine how spatial patterns interact with ecological processes and affect our ability to make generalisations. We sought to address the dichotomy of an understanding of ecological processes based largely on field manipulations and surveys over small scales (e.g. experiments with plot size of <10 m^2 and extents $<10^3$ m^2) versus the need to understand/predict larger scale ecological and environmental issues (e.g. scales of km^2 or whole harbours).

Data collection was an essential component of this workshop; our ideas needed to be embedded in practicalities and assessed empirically. The main aim of this collaborative series of studies was to include spatial scale within studies of pattern and process of a soft-bottom macrofaunal community living in a dynamic sandflat environment. For the workshop, investigators were invited to New Zealand to spend about 2 months working on the sandflats of Manukau Harbour, a site providing considerable background information on factors affecting distributions patterns of macrofauna. The approaches represented by the participants can be classified as: (1) statistical analysis of pattern in relation to scale, (2) experimental analysis of benthic processes, (3) fluid and sediment dynamics of the benthic boundary layer, and (4) numerical modelling to predict large-scale patterns from knowledge of processes at relevant scales. Principally, we attempted to extend the generality of site-specific field studies by incorporating quantitative information on hydrodynamic processes (particularly mechanisms of bed disturbance and the movement of post-larval macrofauna) and by embedding experimental studies into the ambient spatial heterogeneity of dominant macrofauna. In this paper we present a broad overview of the ideas behind the workshop, a general description of the study site, and an outline of the subsequent papers.

Natural history information is important in developing studies which are sensitive to issues of scale because it provides insight into factors that spatially and temporally constrain species (e.g. life cycles, scales of movement and dispersal, resource requirements). Therefore, our first objective was to select a site where as much as possible was known about both the action and interaction of the physical and biological components of the environment. A second criterion was to focus on processes within, rather than among habitats, hence reducing the need for replication across habitats. We also wanted to work on a sufficiently large and representative area so that we could encompass within-habitat heterogeneity to permit generalisation. A final, but nevertheless important, criterion was the maximum sampling effort that we were able to invest in field work. The field site in Manukau Harbour chosen for this workshop met all these criteria, with previous research giving us a comparatively good knowledge of macrofaunal community structure and function and of various physical processes.

3. Study site

The study site chosen for the workshop was the extensive intertidal flats off Wiroa Island in Manukau Harbour (37°01.3′S; 174°49.2′E), New Zealand (Fig. 1). This large (368 km^2) harbour has extensive intertidal areas of which about 40% are intertidal sandflats. The harbour is mesotidal having semi-diurnal tides with mean neap and spring tidal ranges of 2.0 m and 3.4 m, respectively. The intertidal sandflat near Wiroa Island is exposed to the prevailing south-westerly wind with a fetch of 4 km (at mid tide) up to 17 km (at spring high tide). Light to moderate (5–10 $m \cdot s^{-1}$) west and south-west winds commonly blow across the sandflats, producing waves 10–30 cm in height and reworking sediments to a depth of 1–3 cm (Cummings et al., 1995; Dolphin et al., 1995). On the lower reaches of the sandflat, tidal currents are strong with peak flood and ebb velocities of 46 and 33 $cm \cdot s^{-1}$ respectively. Spring flood tide velocities exceed Shields threshold for sediment entrainment (Dolphin et al., 1995). On the middle and upper portions of the sandflat peak tidal velocities are typically under 30 $cm \cdot s^{-1}$. The study 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 diam. and 10–15 cm deep) created by eagle rays

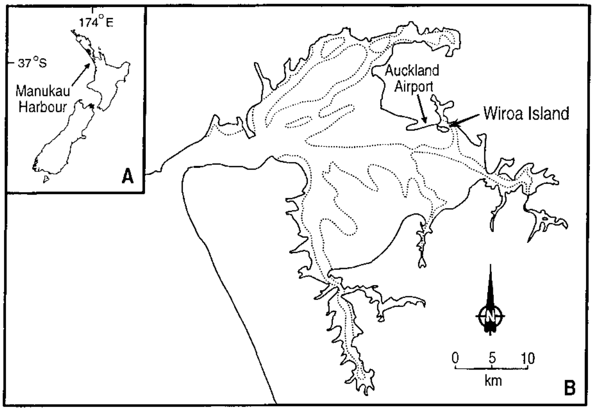

Fig. 1. Location of (A) Manukau Harbour, (B) Wiroa Island, with the extensive intertidal sandflats of Manukau Harbour outlined by dotted lines.

(*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 dominated in terms of both abundance and biomass by bivalves (Pridmore et al., 1990).

4. Previous work

The soft-sediment communities of Manukau Harbour have been previously described (Powell, 1937; Grange, 1977, 1979; Henriques, 1980; Grange, 1982; Roper et al., 1988). Time-series data demonstrate that macrofaunal communities have been remarkably persistent over recent years (Turner et al., 1995). The most relevant descriptions of the Wiroa Island sandflat macrofaunal community are given in Cassie and Michael (1968) and Pridmore et al. (1990). Studies of sedimentary processes have shown that sediment entrainment by strong spring tidal currents is restricted to the lower regions of the intertidal sandflat, while episodic wind-waves (≤ 0.7 m in height) dominate sediment resuspension in the upper intertidal reaches (Dolphin et al., 1995). Field data and hydrodynamic modelling demonstrate that semi-diurnal tides dominate circulation in Manukau Harbour (unpublished data). However, strong winds (≥ 7.5 $m \cdot s^{-1}$) produce residual downwind flows over the intertidal areas which are compensated for by a residual return flow in the main channels. During the workshop, this harbour-wide hydrodynamic model was further refined to derive the tidal current patterns on the Wiroa Island sandflat.

Since 1987, studies have been conducted at the Wiroa Island site and others within Manukau Harbour, to gain an understanding of macrofaunal distribution patterns and how they are influenced by a variety of processes. The macrofaunal community of the

Wiroa Island sandflats is dominated both numerically and in terms of biomass by bivalves, in particular the tellinid *Macomona liliana* Ireland, and the venerid *Austrovenus stutchburyi* (Gray). Polychaetes are less abundant, with the commonest species being *Travisia olens* Ehlers, *Orbinia papillosa* (Ehlers), *Aonidies oxycephala* (Sars) and *Microspio maori* Blake.

Previous studies have focused attention on the processes of disturbance and recovery, biotic interactions, resident mobility and how our perceptions of the role of these processes may be affected by spatial and temporal scales of sampling. The spatial arrangement of common bivalves and polychaetes at six, 9000 m^2, sites around the harbour, including one near Wiroa Island (Thrush et al., 1989), demonstrate a variety of patterns at scales of tens of metres. This scale of heterogeneity has had important implications for sampling design and the development of monitoring programmes (Hewitt et al., 1993; Thrush et al., 1994a). Initial insight into the importance of post-settlement movement by macrofauna came from an assessment of the recolonisation of the large pits created on the intertidal flats by feeding eagle rays. Pits were rapidly recolonised by animals common in adjacent undisturbed sediments (Thrush et al., 1991). The importance of movement by post-settlement *Macomona liliana* emerged as an active emigration response in a pesticide toxicity field study (Pridmore et al., 1991). Subsequent laboratory studies showed juvenile *Macomona liliana* were capable of actively leaving unfavourable sediments even at low shear velocities, and drifting in the water column using byssus threads (Cummings et al., 1993). Bedload and water column traps were used to investigate the dynamics of post-larval dispersal on the Wiroa Island sandflats over a 1.4–16.1 knot range in mean wind velocity (Commito et al., 1995). Strong and positive relationships among wind and water velocity, sediment flux, and post-larval dispersal, especially in the bedload, were demonstrated. Sampling of the water column over this sandflat demonstrated the importance of post-settlement drift of individuals of many common macrofaunal species (Cummings et al., 1995).

Results of these experiments emphasise the potential for high rates of flux of animals associated with wave disturbance of the sandflat. However, these physical processes do not simply swamp biological interactions. On the Wiroa Island sandflat, recolonisation of small defaunated plots is influenced by resident adult infauna. In particular, low adult densities of *Macomona liliana* can facilitate recruitment of conspecifics, while high adult densities can inhibit conspecific recruitment (Thrush et al., 1992, 1996). Evidence of further interactions involving this species came from an experiment designed to assess the effects of large vertebrate predators on macrofaunal community structure (Thrush et al., 1994b). Exclusion of eagle rays and shorebirds resulted in increased densities of large *Macomona* relative to those found in control plots. Samples collected from experimental plots at a time when densities of juvenile bivalves were high following recruitment indicated a negative interaction between adult and juvenile *Macomona*, with similar indirect effects also inferred for a variety of other macrofauna.

In all of these studies experimental plot size (i.e. grain) was small (≤ 4 m^2) and if physical processes alone were important in determining the distribution of post-settlement macrofauna, we would expect local biotic interactions to be swamped. However, we found significant effects in our experiments despite the potential for wind-wave disturbance.

5. Workshop approaches

Our goal was to conduct studies that focused on important features of the sandflat system that were sensitive to issues of scale, and the interplay of both biological and physical processes.

5.1. Analysis of patterns

Our primary intention was to produce a map of the distribution of infauna that would enable us to assess the interdependence of pattern and process within a representative area of sandflat. We focused our attentions on the most dominant species *Macomona liliana*. A preliminary sampling exercise identified appropriate sampling strategies (i.e. determined lag and grain) and coincidentally, enabled us to assess co-occurrence relationships between individuals over various spatial scales (Hewitt et al., 1997). The density of adult *Macomona* was then mapped within a 250×500 m area. The map generated from this grid provided a ‘‘density-scape’’ against which variations in physical and biological conditions could be assessed and into which process studies could be embedded. Specific hypotheses concerned: predator densities relative to macrofaunal densities (Cummings et al., 1997; Hines et al., 1997); post-settlement movement relative to macrofaunal densities (Turner et al., 1997); spatial modelling of macrofaunal densities relative to variations in physical conditions (Legendre et al., 1997).

5.2. Experimental analysis of adult/juvenile interactions and predation in relation to neighbourhood density

A novel design was developed to test adult/juvenile interactions amongst *Macomona* in relation to the neighbourhood density of adult *Macomona* (Thrush et al., 1997). Density variation within the 250×500 m grid was used explicitly for this purpose. Each grid point was assigned a neighbourhood density, which was the mean density derived from the density estimate at that point and in the 8 grid cells surrounding it. This allowed us to assign a quantitative value ($\bar{x} \pm$sd) to each point, rather than having it become a unit within a larger area where the mean density is taken as homogeneous. This differentiates our approach from experiments or surveys which exploit blocking or stratification. Our design uses the density-scape of adult *Macomona* as a continuous description of heterogeneity, hence recognising that variation occurs on all scales and is not just restricted to one scale (i.e. blocks or strata). In other words, neighbourhood density was treated as a ratio scale (regression-type) variable, rather than a nominal (ANOVA-type) variable. The advantages of this design were: (1) results can be scaled up statistically to the entire experimental area, not just to preselected patches; (2) there were no border effects through location of treatments at the edges of patches; (3) the survey data was quantitatively integrated into the experimental design, leading to a tighter coupling of experiment to survey, specifically via generalized linear models (McCullagh and Nelder, 1989) which are more informative than a nominal-scale models.

We also specifically addressed how variations in grain and lag (i.e. size and spacing of replicates) may influence experimental results with a further experiment utilizing a more classical complete randomized block design. This experiment focused on adult/juvenile interactions amongst the second most common bivalve on the sandflat *Austrovenus stutchburyi* (Whitlatch et al., 1997).

5.3. Characterisation of the hydrodynamic regime, and its effects on macrofaunal movement and food supply

The set-up and calibration of models to realistically simulate hydrodynamic processes is non-trivial, involving schematization of the bathymetry over the entire harbour and the collection of current and tide-level data. Collection of physical data and hydrodynamic modelling (Bell et al., 1997) were undertaken because import and export of macrofauna arises from both passive and active movements related to the hydrodynamic regime. Although the relative importance of transport mechanisms operating over a range of advective and diffusive scales cannot be readily determined, the flux of animals and potentially co-varying physical variables could be measured at various points on the spatial grid (Grant et al., 1997; Turner et al., 1997b).

5.4. Synthesis and the modelling of processes

The expectation of this large collaborative study was to develop the ability to predict large-scale patterns from a knowledge of underlying processes. If an acceptable model could be generated and verified then it would be possible to scale-up from our results. We developed two types of models that tested the effects of scale as an extension of our field work: a computer simulation model (McArdle et al., 1997) and a dimensionless ratio scaling model (Schneider et al., 1997).

This, in summary, was the purpose of the NIWA Workshop. We hope the following papers provide some insight into the quantitative synthesis of pattern and process studies (Eberhardt and Thomas, 1991) that enable large-scale predictions to incorporate the small-scale phenomena that can so profoundly influence community structure.

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