Scaling-up from experiments to complex ecological systems: Where to next?

S.F. Thrush[a,*], D.C. Schneider[b], P. Legendre[c], R.B. Whitlatch[d], P.K. Dayton[e], J.E. Hewitt[a], A.H. Hines[f], V.J. Cummings[a], S.M. Lawrie[g], J. Grant[h], R.D. Pridmore[a], S.J. Turner[a], B.H. McArdle[i]

[a]*National Institute of Water and Atmospheric Research, P.O. Box 11-115, Hamilton, New Zealand*
[b]*Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Canada ALC5S7*
[c]*Département de Sciences Biologiques, Université de Montréal, C.P. 6128, succursale Centre-ville, Montréal, Quebéc H3C 3J7, Canada*
[d]*Dept. Marine Sciences, University of Connecticut, Groton, CT 06340-6097, USA*
[e]*Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093-0201, USA*
[f]*Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037, USA*
[g]*Culterty Field Station, University of Aberdeen, Newburgh, AB40AA, Scotland*
[h]*Dept. of Oceanography, Dalhousie University, Halifax, Canada B3H 4JI*
[i]*Biostatistics Unit, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand*

1. Workshop synopsis

The workshop studies encompassed four central themes: characterisation of the hydrodynamic regime and its effects on bivalve movement; analysis of bivalve spatial patterns and the relationships between physics and biota; biotic interactions in relation to spatial scale and heterogeneity; and synthesis and modelling. Many of the findings of our field study depended upon an adequate description of pattern so that changes in spatial scale could be explicitly considered in the context of spatial pattern. The focus on integrating patterns and processes inevitably leads to the issue of scale. If research is to assist in predicting, resolving or mitigating large-scale environmental problems, then we must face the challenge of relating patterns and processes across space and time so that small-scale surveys and experiments can be related to conclusions at larger-scales. This workshop provided an opportunity to take a cross-disciplinary approach to integrate physical and ecological patterns and processes over different spatial scales. In this paper we briefly summarise the workshop's conclusions in relation to this theme and discuss implications for future research.

*Corresponding author.

1.1. Hydrodynamics and its influence on biota

Sandflat morphology, waves and tides influence energy dissipation and sediment transport on the Wiroa sandflat. Even on this extensive sandflat, field observations and hydrodynamic modelling portray a complex picture of sediment transport and highlight the key role of the coupling between wind waves, tidal currents and the tidally-varying water depth in mobilising bed sediments and associated material (Bell et al., 1997). On a day-to-day basis, hydrodynamic conditions are especially important when the water is shallow enough (<20 cm deep at our site) for waves to stir the bed and tidal currents are strong enough to transport resuspended material, including larvae and juvenile infauna. Less frequent events (e.g., storms) that coincide with spring tides can have a major influence on the Wiroa sandflat (Dolphin et al., 1995), but none occurred during the workshop.

Despite the importance of physical processes on the sandflat, hydrodynamic models failed to predict spatial variation of sediment transport within the study site (Grant et al., 1997). The model resolution was probably too coarse to accurately model the influence of topographic features in the vicinity of the study site (Grant et al., 1997). The spatial variability in sediment transport measurements over the study area demonstrated the potential limitation of unreplicated studies, even of largely physically driven processes. Measurements of sediment deposition and erosion around the study site were used as a template for the distribution of post-settlement bivalves. Generally, the areas of greatest sediment deposition and highest juvenile bivalve abundances co-occurred. Nevertheless, sediment flux was not a perfect template for post-settlement bivalve movement. High densities of adult *Macomona liliana* Iredale were correlated with an increased flux of post-settlement bivalves (Turner et al., 1997). The effects of resident adult *Macomona* on juvenile bivalves were species-specific and dependent on hydrodynamic conditions; the negative effects of background *Macomona* density were most consistent during the periods of calm weather.

Matching hydrodynamic processes with biological patterns and processes proved difficult because biological and physical measurements have different frequencies and resolutions. In particular, biota density variations integrated physical events operating on different time scales. Legendre et al. (1997) illustrated how spatial relationships and distributions of different size classes of bivalves were correlated with, and can be modelled by, different environmental processes. The hydrodynamic variables available for analysis (flood and ebb tide shear stresses and work done on the sandflat by waves) were only partly helpful at explaining bivalve distributions. Position variables (elevation and the percentage of time sites were covered by >20 cm of water on spring tides) proved the most useful. Even so, the fraction of variability unexplained by the physical variables remained high (20–90%), especially for smaller bivalves.

1.2. Extrinsic determinants of spatial pattern for infaunal bivalves

Different spatial structures were apparent for adult and juvenile bivalves at the scale of the study site. Large *Macomona* (>15 mm shell length) in particular exhibited a "wave-like" spatial structure with high densities in the north-west corner of the study

site. In contrast, smaller *Macomona* and *Austrovenus stutchburyi* (Gray) (2.5–4 mm shell length) displayed weaker but still significant spatial gradients across the study site (Legendre et al., 1997). Physical variables derived from sampling the study site and from hydrodynamic models were most useful in explaining large-scale variation in the density of adult *Macomona* and *Austrovenus* (Legendre et al., 1997). Principal component analysis and spatial modelling indicated that the importance of physical and biological processes varied for different-sized bivalves across the 12.5 ha study site. Juvenile bivalves were less spatially structured than larger size classes. No significant adult–juvenile interactions were identified by our spatial modelling over the study site. However, multi-scale sampling (1 m–1000 m spatial scales) of the Wiroa sandflat prior to the workshop experimental studies detected both local (< 1 m lag) negative correlations of juvenile and adult *Macomona* and positive associations between adults and juveniles at a lag of 5 m (Hewitt et al., 1997). This preliminary study was important in deciding at what scale the other workshop studies were to be conducted. This is important when, as demonstrated here, our perceptions of adult–juvenile spatial relationships clearly depend on the scale of study.

1.3. Biotic interactions in relation to scale and heterogeneity

Significant negative effects of high densities of adult *Macomona* on juvenile conspecifics and some other infauna were detected in the experimental plots with concurrent relations also apparent at the scale of the study site. The multi-scale study of Hewitt et al. (1997) helps to explain the disparity in the importance of adult–juvenile interactions between the spatial modelling (Legendre et al., 1997) and the manipulative experiment that was nested within the adult *Macomona* density-scape (Thrush et al., 1997b). Over small spatial scales, it appears that juvenile *Macomona* avoid adults, or have low survivorship if close to them. However, over larger spatial scales juveniles and adults prefer similar physical conditions. The effect of experimental and background density variation of adult *Macomona* on juvenile conspecifics (Thrush et al., 1997b) was re-analysed by including the important physical variables identified by Legendre et al. (1997) and the number of juvenile bivalves (averaged over the duration of the experiment) moving with sediment bedload (Turner et al., 1997). The effect of background density variation of adult *Macomona* on juveniles, although reduced in magnitude, was still important (Table 1). Thus, although the intensity and direction of correlation changed with scale and distributions were affected by environmental gradients, small-scale adult–juvenile interactions are apparently nested within larger-scale associations.

Negative adult–juvenile interactions were apparent for deposit-feeding *Macomona*, but less clear cut for the suspension-feeding *Austrovenus*. This is consistent with the literature (see Olafsson et al. (1994) for a recent review). Negative effects of adult *Austrovenus* on recruits were only apparent at densities that reflected the highest densities on the Wiroa sandflat (Whitlatch et al., 1997).

An interesting result of the Whitlatch et al. (1997) experiment was the plot-size-dependent rates of siphon nipping on *Austrovenus*. Flatfish responded to prey patch size even when prey density was quite low. Similarly, eagle rays appeared to respond to the

Table 1
Generalised linear model analyses[a] on the effects of all the physical and biological continuous variables measured at the study site, including experimental and background densities of large *Macomona* (>15 mm shell length), on the number of recruit *Macomona* (<4 mm) collected in experimental plots. Values given are goodness of fit followed by type 3 χ^2 probabilities for the original and the most parsimonious model (– represent factors dropped from this model)

	Original model	Parsimonious model
Deviance/df	1.0214	1.0621
Pearsons χ^2 deviance/df	0.9734	0.9944
	P	P
Experimental *Macomona* density[b]	0.0014	0.0005
Background *Macomona* density[b]	0.0784	0.0053
Bedload traps[c]	0.0364	0.0051
Bedpans (no shell hash treatment)[c]	0.0001	0.0008
Bedpans (shell hash treatment)[c]	0.1490	0.0006
Time covered with >20 cm water[d]	0.1408	–
Location—North[d]	0.1509	–
Location—East[d]	0.6682	–
Elevation[d]	0.1282	0.0394
Elevation squared[d]	0.1246	0.0320
Elevation cubed[d]	0.1263	0.0223
Current velocity ebb[d]	0.1801	–
Current velocity flood[d]	0.8514	–
Shell hash[d]	0.0540	0.0001
Wave stirring[d]	0.0892	0.0113
Wind—SW[d]	0.4564	–
Wind—WSW[d]	0.2446	–
Total df	75	75

[a]See Thrush et al. (1997a) for reference to statistical modelling technique.
[b]Factors derived from Thrush et al. (1997a).
[c]Factors derived from Turner et al. (1997).
[d]Factors derived Legendre et al. (1997).

natural density patterns of bivalve prey (adult *Macomona*) within the study site. Hines et al. (1997) demonstrated a significant increase in the rate of predation by eagle rays at a threshold of adult *Macomona* above 180 m^{-2}. In contrast, there was no evidence of aggregative response to prey patchiness at the scale of the study site or smaller for wading birds (Cummings et al., 1997). Longer term studies are needed to determine the effects of vertebrate predators on the Wiroa sandflat macrobenthic community (Thrush et al., 1994). Nevertheless, adult *Macomona* in areas of low density gain a refuge from predation and disturbance by eagle rays which will tend to stabilise prey populations and even out prey distributions (Hines et al., 1997).

1.4. Modelling processes over different scales

Combining available information on settlement, ageing, movement and mortality, McArdle et al. (1997) developed a spatially explicit *i*-state numerical model (Caswell and John, 1992) to assess whether local biological processes could account for the

large-scale (ca. 100 m) spatial patterns of the adult *Macomona*. The results of this model are consistent with Legendre et al. (1997), which found no support for the role of small-scale biological processes in determining the large-scale spatial arrangement of *Macomona*. When considering the role of local biotic interactions in generating large-scale patterns, the specifics of the biological processes are important. The biology of *Macomona* we observed did not conform to the ''Neighbourhood Coherence Principle'' (Phipps, 1992). Movement by juvenile *Macomona* and eagle ray predation work to smooth-out spatial patterns in adult *Macomona* abundance. Small-scale interactions cannot be simply extrapolated to larger-scales by direct multiplication because different processes are likely to prevail at larger-scales.

Schneider et al. (1997) developed a graphical technique that enables the scope of experiments and surveys to be compared with models and theory. This procedure is a very useful starting point in any field programme because it focuses attention on the spatial aspects of study design [i.e., grain, lag, extent (see Thrush et al. (1997b) for references)] and readily identifies the level of extrapolation in results. This facilitates an iterative cycling between experimentation and theory by focusing attention on levels of extrapolation.

2. Ecology of benthic communities: integrating the issue of scale

2.1. Linking patterns and processes and making predictions

There does not appear to be one right way to relate patterns and processes across scales. Simply adding or multiplying the effects identified in small-scale studies is problematic (O'Neill and Rust, 1979; Welsh et al., 1988). Rastetter et al. (1992) emphasise the need for caution in summing small-scale processes to model large-scale phenomena because of the errors that can arise due to variation among aggregated components. Moreover, processes operating at large-scale are not always the same as those operating at small-scale. So you could sum small-scale processes forever and yet predict nothing concerning larger-scale effects. Variance is also likely to change with scale. For both the classical and geostatistical estimators variance is inversely related to the size of the sampling units. Changing the extent of a study also changes the variance because physical control becomes more and more variable as the extent increases. Changing the observed variance by changing sampling grain and extent thus, changes our perception of what is more or less important in terms of sources of variation. Nevertheless, developing ways to integrate small-scale experimental studies into larger-scale spatial mosaics is essential to predict large-scale effects (Wiens et al., 1993). The most promising strategies for spatial scaling involve a combination of empirical data collection, prediction and testing (Schneider, 1994). Root and Schneider (1995) independently reached a similar conclusion by comparing different research strategies that have been used to link effects on ecological systems across broad scales in space and time. They refer to a process of ''strategic cyclical scaling strategy'' in which large-scale associations are used to focus small-scale investigations. Iterative checking among pattern, process and prediction has been a consistent theme (Rastetter et al.,

1992; Wiens et al., 1993; Schneider, 1994; Root and Schneider, 1995; Schneider et al., 1997).

Scale is a particularly important issue in marine benthic ecosystems because oceanographic processes influence marine communities over a variety of space and time scales (Barry and Dayton, 1991). Dayton and Tegner (1984) emphasised the enormity of scaling-up implied by generalities based on small-scale experiments in marine benthic systems. Their paper integrated knowledge of processes studied for short time periods with events operating over much longer time scales. They emphasised the importance of using natural history information and observational studies to help design specific process experiments and to put the results of such studies into a broader perspective.

Recognition of the importance of physical processes as external forcing functions that contribute to heterogeneity in ecological systems has a long history. Significant relationships do exist between benthic community composition and physical variables (e.g., Warwick and Uncles, 1980; McLachlan, 1990; Warwick et al., 1991) and they provide an important first-order prediction of large-scale changes. While there is a danger that studying fine-scale dynamics can be irrelevant at the larger-scale (Hall et al., 1994), local biological processes may have emergent properties at larger-scales often through interactions with physical processes. If ecological patterns and processes were easily predicted from physical forces alone then we would be much further ahead in extending generalities and having confidence in predictions. Emergent properties of local biological interactions were not apparent in our workshop probably because species capable of modifying habitats through long-term changes in sediment topography were not important.

Heterogeneities in ecological systems are often generated by local processes interacting with the extremes in physical variables. For example, although sediment disturbance by individual deposit feeders is very localised, the sedimentary fabric can be predisposed to resuspension and erosion during storms with the associated loss of fauna on much larger-scales (Mills, 1969; Gray, 1974; Eagle, 1975; Rees et al., 1977; Rhoads et al., 1977). Conversely, small-scale polychaete tube-mats can reduce erosion by helping to stabilise sediments (Thrush et al., 1996). Pacala and Deutschman (1995) provided a good illustration of how small-scale details do matter when attempting to model large-scale phenomena. Their forest simulation models and field data demonstrated that local processes controlling spatial heterogeneity at the scale of individual trees can have large effects on ecosystem and community level properties (standing crop, successional species turnover). While most marine benthic organisms are not as long-lived or sedentary as trees, weak interactions and indirect effects are probably pervasive, although difficult to detect, and are likely to be important influences on ecosystem and community level properties (e.g., Underwood et al., 1983; Peterson and Black, 1988; Fairweather, 1990; Hall et al., 1990; Wootton, 1994; Menge, 1995). Ecological systems, with non-linear interactions, feedbacks, lags and priority effects, exhibit the characteristics of complex systems (Costanza et al., 1993; Cowan et al., 1994; Perry, 1995).

Natural history information is essential to integrate studies across space and time scales. Reproductive rates, life cycles, scales of movement, behaviour and resource requirements for different life-stages all play important roles in how species respond to environmental heterogeneities on different scales. Basic information on body size,

mobility and feeding mode can also be used to predict successfully small-scale (6 m extent) spatial arrangements (Hewitt et al., 1996). Natural history information can also highlight limitations of ecological theory based on other systems. For example, in terrestrial systems it has been proposed that highly mobile organisms are likely to be less sensitive to small-scale patchiness than more sedentary species (Kotliar and Wiens, 1990; Milne, 1991). While some observations of predation by large vertebrates made during the workshop agree with this suggestion (Cummings et al., 1997; Hines et al., 1997), other processes, such as habitat selection or differential survival by the highly mobile juvenile *Macomona*, do not (Hewitt et al., 1996; Turner et al., 1997).

2.2. Heterogeneity, scale and difficulties with study design and interpretation

Experimental marine ecology has relied heavily on statistical methods developed for laboratory and agricultural research. One of the reasons field experiments are powerful ecological tools is that they provide the potential for strong inference (Hairston, 1989). But there are problems with heterogeneity, determining the ''right scale'' for experiments and the effect of changes in scale on experimental results. Hypothesis testing is important, but there is a risk of losing the larger-scale, and omitting important processes through a focus on certainty and single processes. Large-scale experiments are valuable and relevant (Carpenter, 1996), but they are not always feasible.

Ecological field experiments are conducted in heterogeneous environments that are not necessarily ecologically neutral. Interactions between experimental manipulations and background conditions can occur (Thrush et al., 1997a). There are developments in experimental design both to account for and incorporate heterogeneity. For example: Dutilleul (1993) provides analysis of variance designs for ecological field experiments that account for different types of spatial heterogeneity; Ver Hoef and Cressie (1993) describe analytical procedures using natural spatial variation to help determine treatment contrasts in field experiments; and Fortin and Gurevitch (1993) describe techniques to detect spatial autocorrelation and distinguish its effects from treatment effects in experiments.

Categorical analytical approaches implicitly focus the experimental design on finding the ''right scale''. In fact at the start of the workshop we spent many days trying to identify the scale of different processes that might be at work on the sandflat. This was a dead end since there was no characteristic scale for this study. Recognising that different processes are relevant at different scales and that processes may operate in different ways at different scales draws our focus away from a solely reductionist approach. Rather than asking ''what is the right scale?'', we should ask ''how do we go from one scale to another?''.

Changing the scales over which data are collected, involves changing sampling grain, lag or extent. Focusing on these three components can help us define how the importance of processes change with scale and recognise the degree of extrapolation possible from individual studies. Extending the results of studies by spatial scaling has two components; extending the generality of the results to different places (i.e., changing the spatial extent) and extending the size of the area to which the phenomena are applied (i.e., changing the spatial grain). Experiments manipulating grain have proved to be

insightful. For example, recolonisation of defaunated plots of sediments in both sheltered mudflats (Smith and Brumsickle, 1989) and exposed sandflats (Thrush et al., 1996) have revealed significant scale-dependent recovery, even though the plot sizes were small and only manipulated changes in grain over about one order of magnitude. Estimates of rates of sub-lethal predation by flatfish on *Austrovenus* were found to be highly dependent on plot size (Whitlatch et al., 1997), and eagle rays foraged in patches of adult *Macomona* on certain spatial scales (Hines et al., 1997). The extent of a study has a crucial influence on what processes appear important in determining species distributions, as demonstrated by spatial modelling of our study site (Legendre et al., 1997). Simply extending experiments or surveys to identify the generality of response is insufficient unless the many potential confounding factors likely to vary with extent can also be incorporated into the experimental design.

Grain, lag, extent and scope thus have important implications for study design and interpretation. Adding in treatments that manipulate any spatial or temporal components of sampling scale can hugely complicate the experimental design and limit the allocation of effort. Nevertheless, because our results are likely to be scale-dependent (Schneider, 1994; Schneider et al., 1997), we need to be more explicit about scale in the design of experiments and surveys so that we can more clearly recognise the degree of our extrapolation and generalisations. To identify how local processes are modified by changing environmental conditions, important environmental gradients can be incorporated into the study design. This can lead to greater sensitivity of analytical techniques and extend the ecological significance of experimental results (Dayton, 1971; Underwood et al., 1983; Keddy, 1991; Ellis and Schneider, in press).

The limitations of inferences drawn from different types of studies need to be appreciated and balanced against the range of scales of observation (Eberhardt and Thomas, 1991; McArdle, 1996). What is required is a quantitative synthesis of pattern and process studies. For instance, knowledge of nested spatial patterns allowed us to estimate suitable sampling intervals, essential to establishing relationships between spatial patterns and ecological phenomena (Hewitt et al., 1997). By embedding our experimental plots within the natural density-scape of adult *Macomona* within our study site, we were able to match grain to process (Thrush et al., 1997a). The extent of the study improved confidence in our results. Furthermore the 250×500 m study site was equivalent in size to grid cells of large-scale models, allowing us to bridge the gap between flux and demography (Schneider et al., 1997). Thus, the multiple approaches used in the workshop provided information about a number of different spatial scales and processes.

3. Future directions

While the literature on the issue of scale in ecology has burgeoned in recent years, there is little practical advice to help field ecologists develop studies that enhance generalisation. Experimental results cannot be scaled upward according to area because not all concomitant rates scale with area in the same way. Thus, most experiments are not accurate scale models of larger-scale processes. Without the development of spatial

scaling rules (e.g., $Rate = (Area)^b$) to link local processes to larger-scale phenomena, we risk omitting some critical mechanisms. But as yet there is no history of formal spatial scaling in ecology (Schneider, 1994). In the absence of such rules we have to rely on formalised intuition as in the rate diagrams of Schneider et al. (1997). Inevitably this technique will be limited because we may expect non-linearities in scaling-up problems (He and Legendre, 1996). Nevertheless the use of rate diagrams is an important start toward a rigorous and quantitative assessment of the extent to which individual studies can be scaled-up.

We need to develop further methods that combine observations of system phenomena with experimentation on limited parts of the system (Wiens et al., 1993). A variety of tools is needed to understand ecological systems and improve our ability to extrapolate and generalise. In marine soft-sediment systems, techniques are available that enable us to broadly map habitat types (e.g., high resolution sonar and video images) and this can be combined with infaunal sediment sampling through the development of multi-resolution sampling techniques. Geostatistics may then be used to link the large-scale variability apparent in maps through proxy variables to the results of small-scale experiments. To link results across scales will require a more multidisciplinary approach focusing on the integration of different studies that emphasise different processes and scales of heterogeneity. Where the direct linking of pattern and process at different scales (Thrush et al., 1997a) is not possible, different studies may be combined by careful meta-analysis (Arnqvist and Wooster, 1995). Meta-analysis has the potential to enable a weighting of individual studies dependent on the scale over which they have been conducted. Ecologists are attuned to the problems of replication in the design of individual studies, now it is essential that the issue of scale and representativeness also be treated in such a rigorous fashion.

4. Conclusions

In all of our recommendations we emphasise the need to produce predictions relevant to the large-scale. Unfortunately this is often at variance with the need for confidence in results. Confidence is normally gained by increasing replication with a concomitant increase in effort, whereas generality of results is often gained by increasing sample separation. Developing strategies that nest different sampling techniques with different levels of resolution can help provide confidence in the representiveness of results. We must carefully and explicitly evaluate the trade-offs between confidence and generality, because too much emphasis may be placed variously on certainty (learning more and more about less and less) or generality (learning less and less about more and more).

One "test" of our understanding of benthic community structure and function is to provide information and solutions to environmental managers. Studies at the scale of environmental management have important benefits by integrating science into the management process (Walters and Holling, 1990; Holling, 1996). In order to address issues of harbour-wide, regional, or global change we need to be able to answer questions of how large-scale processes will influence ecological processes on local scales and how these effects will vary from place to place. Identifying the limits to

extrapolation from small-scale studies, how processes interact across scales, and how we develop techniques for incorporating scale into ecology and environmental management are important, exciting and challenging questions facing both ecologists and environmental managers.

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