

6 Conclusions and future work

In this thesis my emphasis has been to integrate measurements and theoretical understanding into a quantitative modelling framework. The aim has been to better understand the interaction between burrowing animals and the sediments they inhabit, and the macroscale biogeochemical consequences of this interaction. A further aim was to explore the ability of current theoretical understanding (as captured in models) to predict the outcome of these animal-sediment interactions.

The bioturbation and bioirrigation models used in this work serve useful diagnostic functions in at least four ways:

1. they provide a method for testing whether current theoretical understanding matches experimental observations (for example, the nitrogen modelling in Chapter 5 highlighted significant differences in theoretical understanding and measurements in three thalassinidean shrimp experimental studies);
2. they allow the exploration of system sensitivity to underlying processes (for example, the sensitivity analyses conducted in Chapter 3 using maximum likelihood methods generated confidence bounds on sediment mixing parameters);
3. they allow specific hypotheses to be tested (for example, the nitrogen modelling in Chapter 5 was used to explore the possibility that irrigated burrows may be responsible for high denitrification rates in Port Phillip Bay); and
4. they provide a method for identifying important knowledge gaps that need to be addressed in future work.

A further model use is to aid experiment design, both by drawing attention to implications of design decisions (such as the use of narrow tanks) and by clarifying measurement priorities (for example, the importance of determining mass budgets and quantifying flows between pools of nutrients).

Conclusions specific to each section of work are reviewed here, followed by more general suggestions for the future.

6.1 *Laser scanner experiments*

A laser scanner was used to create a time series of three-dimensional maps of sediment mounds created by burrowing shrimp, *Trypaea australiensis*. The use of a laser scanner is a novel approach to this problem, and a particular advantage is its accuracy in measuring volumes expelled to and subducted from the sediment surface. The laser scanner experiments of *Trypaea australiensis* burrow mounds represented a more detailed study of mound dynamics than is usually possible by sediment trap or tracer core methods. Results from these experiments pointed to two clear conclusions: the rate of material falling back down into a burrow can be just as significant as the rate at which sediment is being expelled through the burrow opening; and the exchange of material between surface and depth represents a rapid oscillation that will not be detected if data is collected at low sampling frequencies. I have found no discussion on either of these points in the literature. These results raise questions about appropriate measurement approaches in the field, and also suggest that rapid two-way non-local transport needs to be included in sediment mixing models for sediments inhabited by thalassinidean shrimp.

6.2 *1-D EIC model*

The laser scanner results were the motivation for the development of the Excavate, Infill and Collapse (EIC) model. This simple non-local model for sediment mixing by biota is a combination of the upward-conveyor belt and burrow-and-fill models; the model includes excavation of material to the surface, the collapse of burrows and the burrow infill with surface material. Maximum likelihood estimation and model comparison techniques demonstrated that the EIC model performed better than the diffusion model in modelling radionuclide cores from Port Philip Bay (PPB). In all PPB cores, the best EIC model parameter estimates required some level of burrow infill, which offers further evidence of the importance of subsurface injection of surface material. A significant advantage of this model over the diffusion model is its ability to produce a broader range of profiles while capturing the important non-local exchanges between the sediment surface and depth. Further model testing involving porosity variation and non-uniform burrowing with depth suggested that these alterations make significant differences to model results.

6.3 *Higher dimensional EIC model*

The EIC model was expanded to two and three dimensions to demonstrate its usefulness as a simple mechanism for introducing lateral heterogeneity to model sediments. Significant heterogeneity occurs in real sediments and is thought to have first order impacts on biogeochemical processes. The 2-D EIC model was used to generate a synthetic data set in order to perform a critical assessment of the scope for extracting actual mixing parameters from one-dimensional cores. This work demonstrated that even when the underlying mixing process is known exactly, heterogeneity and sampling procedures can confound reliable recovery of the original mixing parameters.

A valuable extension to the higher dimensional EIC model would be to couple it to the automatic burrow generation routine developed by Koretsky et al. (2002). Detailed resin casting of burrow networks could provide good data for creating more realistic burrow maps.

The equations of the 2-D or 3-D EIC model could be applied equally well to porewater species, so allowing the possibility of multi-dimensional solid and porewater modelling. Such a model could be used to investigate how sediment diagenesis is altered by the simultaneous introduction of pockets of organic matter and oxygen to depth in the sediment.

6.4 *Burrow irrigation modelling*

The burrow irrigation modelling work combined two well-accepted modelling approaches (radially symmetrical burrow geometry and a nitrogen diagenesis model) to investigate the impacts of burrow irrigation on sediment nitrogen chemistry. Comparison with data from three published thalassinidean experimental studies served to illustrate the model's use in interpreting experimental data, and its ability to explore the extent to which current theoretical understanding, as encapsulated in the model, can explain the measurements. Resolving the divergences between theory and observation are potentially fruitful areas for further work. For example, the model was unable to explain both low ammonium concentrations and relatively small oxygen penetration distances measured in sediment surrounding *Callianassa truncata* burrows. Conversely, the model predicted higher nitrate and lower ammonium levels than measured within *Callianassa japonica* and *Upogebia major* burrows. The model demonstrated that assumptions about diffusive transport through sediment are unable

to explain the rapid changes in oxygen measured in the sediment surrounding a *Callianassa subterranea* burrow.

The model predicts that concentration measurements made in thin tanks will not represent *in situ* burrow concentrations, even if the animal has been established in sediment taken from its native environment. In particular, tank geometry determines the extent to which species such as ammonium can accumulate within the sediment. There are robust theoretical grounds for drawing this conclusion, and experiments aimed at testing and exploring these effects further are needed to ensure these artefacts do not confound future experimental results.

The irrigation model was used to estimate the depth and density of irrigated burrows required to explain high denitrification rates measured in Port Phillip Bay sediments. Model geometry could be configured to match a comprehensive range of data from the Bay, but the geometry and the flushing rates were not consistent with typical thalassinidean shrimp population densities and burrow flushing rates. I conclude that while irrigated burrows can contribute significantly to high denitrification rates, the relatively sparse deep burrows of thalassinidean shrimp are unlikely to be sufficient to explain the full extent of these rates. Further work is needed to more fully understand the nitrogen dynamics within Bay sediments. Resin casting of Bay sediments could be used to reveal the nature of the burrow networks. Dense burrows of other species in the surface layer, and commensals' burrows extending out from thalassinidean shrimp burrows would provide further explanation for the observed denitrification rates. Another possibility includes further investigation into the role of microphytobenthos residing on the sediment surface.

Limitations of one-dimensional representations of nitrogen diagenesis were explored via comparisons between the 1-D models and the full cylinder model. Nitrogen chemistry surrounding a burrow is a genuinely three dimensional problem and any one-dimensional approach will suffer significant drawbacks. For example, the one-dimensional radial model of sediment surrounding a burrow is only appropriate at depths from the sediment surface exceeding approximately 10 cm. Within the upper 10 cm, the direct and indirect effects of the sediment surface have profound impacts on the fluxes between the sediment and overlying water. More work is needed to ascertain the circumstances under which lower dimensional models are appropriate.

6.5 *Future work*

The importance of sediment biogeochemical processes in coastal systems is well recognised, and there are continuing efforts to measure, model and better understand their role in our waterways. The development pressure on these systems is substantial (most people in Australia live near estuaries) and models are increasingly called upon to make specific predictions to guide decision-making in the real world. For example, the Port Phillip Bay Environmental Study developed a water quality model for the Bay to test and assess management scenarios. Yet it is clear that the modelling capability falls well short of that required for robust predictions; in Port Phillip Bay our capacity to explain and model the measured denitrification rates remains limited, yet the ability of Port Phillip Bay sediments to denitrify incoming nutrient loads holds an important key to its ecological health.

Around the world there are continuing improvements to the transport assumptions underlying sediment diagenesis models. In particular, there is growing adoption of higher-dimensional models that allow the representation of lateral heterogeneity. Conclusions in the previous section point to some specific future developments that would make welcome contributions. In addition, further work in the following more general areas would be valuable.

1. Clear procedures for identifying and propagating uncertainty in models are needed quite urgently as a means of assessing model reliability. The already considerable work on parameter estimation techniques needs to be expanded to encompass more aspects of the modelling process. These tools are needed to better understand what the predictive capability of a model really is, and to determine when a new model represents a genuine advance over existing models.
2. The most comprehensive biogeochemical models are complicated, and are often impractical to link to full transport models that resolve a water body spatially. Modellers face inevitable trade-offs between complexity, computability and reliability. More work is needed to ascertain the circumstances under which we can safely model spatial averages only, and when higher-dimensional descriptions are necessary. More broadly, this is a question of determining the level of model detail required to capture the system behaviour of interest. There is always a need to find the simplest model that will perform the required task well.

3. Questions of feedback between the animal behaviour and sediment environment were not addressed in this work, yet are extremely important. Animal-induced alterations to the sediment can serve to improve the animals' circumstances (Aller's cylinder model demonstrated that by crowding together burrowing animals make it easier to detoxify their environment). The reverse could also apply, where once population levels fall below a critical density it becomes harder for the population to remain viable, as the extra effort required to modify their environment through burrow irrigation becomes prohibitively expensive. Another important interaction is that deposit feeders do not merely passively transport organic matter but actively 'mine' it from the sediments. Another example is that in high sedimentation environments some benthic animals react by increasing their burrowing activity, yet in my EIC model I assumed burrowing rates were independent of sedimentation rate. These points need to be considered in bioturbation models.
4. I would like to see future collaborations between experimentalists and modellers nurtured and encouraged for the benefit of both parties, and so that knowledge advances more effectively. Experimentalists' contribution to my work has been immeasurable. In return, insights gained from modelling can provide valuable feedback on experimental procedures, the design of future experiments and the interpretation of results. The complexity of biogeochemical interactions is such that modelling approaches are required to disentangle them.