

Benthic Bulldozers and Pumps: Laboratory and Modelling Studies of Bioturbation and Bioirrigation

Nicola Jane Grigg

February 2003

A thesis submitted for the degree of Doctor of Philosophy of The Australian
National University.

Declaration

The work in this thesis is my own, unless stated otherwise. My research was conducted in the Pye Laboratory, CSIRO Land and Water. None of the material has been submitted towards a degree in any other institution.

Nicola Grigg

Acknowledgments

“She tells herself that thought takes time and there’s nothing you can do about it. Or what in general they stupidly call creation. That doesn’t much resemble streams. Ponds, rather. You flounder in them. It goes nowhere, it’s not happy, not communicative.” *Postmodern Fables*, Jean-François Lyotard.

Unhappy floundering is a common experience among PhD students, and I’ve been no exception. I wish I could say that my slow thinking was focussed on my PhD research; unfortunately I was embroiled in the usual issues that trouble us in our mid-twenties – how to live, and why. Growing environmental problems at local to global scales concern me greatly, as do the glaring differences in quality of life around the world. I feel useless in the face of such enormous issues.

It was against this rather gloomy backdrop that all the following people provided invaluable support during my research.

Ian Webster and Phillip Ford are wonderfully generous people, in spite of the considerable pressures on them. Phillip and Ian have been the most patient and helpful of supervisors, and I am grateful for all the time and energy they have spent guiding me through my work. I particularly appreciated their sharp scientific insights and calm confidence in my ability. Ian White at ANU was always enthusiastic about my work and I welcomed his encouragement and guidance, as well as his assistance with the administrative hoops that needed to be jumped along the way.

The workshop staff (Peter Morphett and Craig Webber) and Pye Lab technicians (Garry Miller, Dale Hughes, Mark Kitchen and Chris Drury) were a pleasure to work with, and I was always impressed at their ability to transform my hazy descriptions into useful experimental equipment or advice. I’m grateful to the IT staff for keeping my computer functional, and for making it so easy for me to work on my thesis from home, yet still remain in contact with the lab.

My office is situated in the Pye Lab, which is home to a wonderful collection of people, many of whom have helped me with my work and my ever-changing world view. Countless other people aided me in surprising ways throughout my project. As just one example, Mike Grace sat and discussed PhD blues with me around a group campfire at an ASL conference in the early stages of my PhD.

My friends, mostly met through UWA, ANU, CSIRO and birthing classes, have all been invaluable, and I’m grateful for the fun, encouragement and advice they’ve provided so consistently throughout my PhD.

My daughter, Zoe, was born 3 ½ years into my project and she’s been a wonderful addition to my life. Pregnancy and looking after a young baby has reinforced in my mind the value of good sleep, food and exercise. Without Zoe I would not have had the determination to give these simple needs the attention they deserve. Thanks to Zoe, I also discovered the joys of working part-time.

Warmest thanks to my parents. They were generous with their love and support, and provided financial help once my scholarship had ended and savings had been diminished.

Brett, my husband, somehow managed to set up and run our vegie gardens, work part-time, look after Zoe part-time and supply an endless stream of lovingly prepared meals throughout my PhD. Thanks B :-)

I’d like to thank my funding sources. My living allowance was funded by an Australian Postgraduate Award. Supervision, technical support, computers, lab and office space were all provided by CSIRO Land and Water, Canberra. The Centre for Resource and Environmental Studies at ANU and the Water Research Foundation provided supervision and funding for field and laboratory expenses.

Abstract

Aquatic sediments are the recipients of a continual rain of organic debris from the water column. The decomposition reactions within the sediment and the rates of material exchange between the sediment and water column are critically moderated by the transport processes within the sediment. The sediment and solute movement induced by burrowing animals – bioturbation and bioirrigation – far exceed abiotic transport processes such as sedimentation burial and molecular diffusion. Thalassinidean shrimp are particularly abundant burrowing animals. Living in high density populations along coastlines around the world, these shrimp build complex burrow networks which they actively maintain and irrigate.

I used a laser scanner to map thalassinidean shrimp (*Trypaea australiensis*) mound formation. These experiments measured rapid two-way exchange between the sediment and depth. Subduction from the sediment surface proved to be just as important as sediment expulsion from depth, yet this is not detected by conventional direct entrapment techniques. The experiments demonstrated that a daily sampling frequency was needed to capture the extent of the two-way exchange.

I derived a one-dimensional non-local model accounting for the excavation, infill and collapse (EIC) of burrows. Maximum likelihood analyses were used to test the model against ^{210}Pb and ^{228}Th profiles taken from sediment cores in Port Phillip Bay, Melbourne. The maximum likelihood approach proved to be a useful technique for quantifying parameter confidence bounds and allowing formal comparison with a comparable biodiffusion model. The EIC model generally outperformed the biodiffusion model, and in all cases best EIC model parameter estimates required some level of burrow infill with surface material. The EIC model was expanded to two and three dimensions, which allowed the representation of lateral heterogeneity resulting from the excavation, infill and collapse of burrow structures. A synthetic dataset generated by the two-dimensional model was used to demonstrate the effects of heterogeneity and core sampling on the mixing information that can be extracted from one-dimensional sediment core data.

Burrow irrigation brings oxygenated water into burrow depths, and can affect the nitrogen cycle by increasing the rates of coupled nitrification and denitrification reactions. I modelled the nitrogen chemistry in the annulus of sediment surrounding an irrigated burrow using a radially-symmetrical diffusion model. The model was applied to three published case studies involving thalassinidean shrimp experiments and to field data from Port Phillip Bay. The results highlighted divergences between current theoretical understanding and laboratory and field measurements. The model further demonstrated potential limitations of measurements of burrow characteristics and animal behaviour in narrow laboratory tanks. Activities of burrowing animals had been hypothesised to contribute to high denitrification rates within Port Phillip Bay. Modelling work in this thesis suggests that the model burrow density required to explain these high denitrification rates is not consistent with the sampled density of thalassinidean shrimp in the Bay, although dense burrows of other animals are likely to be important. Limitations of one-dimensional representations of nitrogen diagenesis were explored via comparisons between one-dimensional models and the full cylinder model.

Table of Contents

1	INTRODUCTION	1
1.1	PORT PHILLIP BAY ENVIRONMENTAL STUDY	1
1.2	ANIMAL-SEDIMENT INTERACTIONS	3
1.2.1	<i>The Thalassinidea</i>	5
1.2.2	<i>Thalassinidean bioturbation</i>	6
1.2.3	<i>Modelling bioturbation</i>	8
1.2.4	<i>Thalassinidean bioirrigation</i>	11
1.2.5	<i>Bioirrigation modelling</i>	12
1.3	AVERAGING IN HETEROGENEOUS ENVIRONMENTS	14
1.3.1	<i>Altered reaction zonation</i>	15
1.3.2	<i>Diffusion in one, two and three dimensions</i>	16
1.3.3	<i>Uncertainty due to the random nature of sediments</i>	17
1.3.4	<i>Summary</i>	18
1.4	THESIS STRUCTURE AND AIMS	18
2	LASER SCANNER MEASUREMENTS OF <i>TRYPAEA AUSTRALIENSIS</i> MOUND TOPOGRAPHY	21
2.1	INTRODUCTION	21
2.2	EXPERIMENT DESCRIPTION	22
2.3	DATA ANALYSIS	26
2.3.1	<i>Calibration</i>	26
2.3.2	<i>Map construction</i>	26
2.3.3	<i>Individual mound analysis</i>	32
2.4	RESULTS AND DISCUSSION	35
2.4.1	<i>General Observations</i>	35
2.4.2	<i>Volume estimates</i>	37
2.5	CONCLUSIONS.....	47
3	ONE-DIMENSIONAL SEDIMENT MODELLING: EXCAVATION, INFILL AND COLLAPSE	49
3.1	INTRODUCTION	49
3.2	MODEL DERIVATION	50
3.3	PHYSICAL INTERPRETATION AND TYPICAL BEHAVIOUR	59
3.3.1	<i>Effect of parameter values in the EIC model</i>	59
3.3.2	<i>Comparison between the EIC and diffusion models</i>	62
3.4	CASE STUDY: PORT PHILLIP BAY ²¹⁰ Pb AND ²²⁸ Th PROFILES	66
3.4.1	<i>Problem description and parameter estimation method</i>	66
3.4.2	<i>Results of Maximum Likelihood analysis</i>	70
3.4.3	<i>Model Assumptions</i>	79
3.5	CONCLUSIONS.....	83
4	HIGHER-DIMENSIONAL EIC SEDIMENT MODEL	87
4.1	INTRODUCTION	87
4.2	TWO-DIMENSIONAL MODEL EQUATIONS	88
4.3	SAMPLE MODEL OUTPUT AND COMPARISONS WITH 1-D MODEL	91
4.4	PORT PHILLIP BAY PROFILES	95
4.5	THREE-DIMENSIONAL MODEL	101
4.6	OTHER CONSIDERATIONS	102
4.6.1	<i>Nonlinear reaction terms</i>	102
4.6.2	<i>More realistic burrow maps</i>	104
4.6.3	<i>More realistic descriptions of burrow collapse</i>	105
4.6.4	<i>Scale issues</i>	105
4.7	CONCLUSIONS.....	105
5	MODELLING NITROGEN DYNAMICS AROUND A BURROW	107
5.1	INTRODUCTION	107
5.2	BACKGROUND	107
5.3	MODEL DESCRIPTION	109

5.4	GENERAL MODEL BEHAVIOUR	115
5.5	THALASSINIDEAN SHRIMP CASE STUDIES.....	122
5.5.1	Case 1: modelling <i>Callinassa truncata</i> field data (Ziebis et al. (1996)).....	122
5.5.2	Case 2: modelling <i>Callinassa subterranea</i> laboratory data (Forster and Graf (1995))	129
5.5.3	Case 3: modelling <i>Callinassa japonica</i> and <i>Upogebia</i> major laboratory measurements (Koike and Mukai (1983)).....	136
5.5.4	Summary of thalassinidean shrimp cases.....	143
5.6	PORT PHILLIP BAY	144
5.6.1	One-dimensional radial model.....	147
5.6.2	5 species cylinder model	159
5.6.3	Summary	165
5.7	CONCLUSIONS	166
6	CONCLUSIONS AND FUTURE WORK	169
6.1	LASER SCANNER EXPERIMENTS	170
6.2	1-D EIC MODEL	170
6.3	HIGHER DIMENSIONAL EIC MODEL	171
6.4	BURROW IRRIGATION MODELLING	171
6.5	FUTURE WORK.....	173
7	APPENDIX: A NOTE ABOUT NON-LOCAL IRRIGATION MODELS.....	175
7.1	BACKGROUND	175
7.2	TO WHAT EXTENT IS EQUATION (7.6) VALID?	179
7.3	VALIDITY OF USING A CONSTANT VALUE FOR α	181
7.4	CAN A NON-LOCAL MODEL DESCRIBE A MULTIPLE-SPECIES SYSTEM WELL?	183
7.5	SUMMARY	188
8	REFERENCES.....	191