

University of Wollongong Research Online

University of Wollongong Thesis Collection

University of Wollongong Thesis Collections

2008

Confronting the challenges of tidal flat conservation: spatial patterns and human impacts in a marine protected area in southern NSW, Australia

Pia C. Winberg Dr University of Wollongong, pia@uow.edu.au

Recommended Citation

Winberg, Pia C, Confronting the challenges of tidal flat conservation: spatial patterns and human impacts in a marine protected area in southern NSW, Australia, PhD thesis, School of Biological Sciences, University of Wollongong, 2008. http://ro.uow.edu.au/theses/123





NOTE

This online version of the thesis may have different page formatting and pagination from the paper copy held in the University of Wollongong Library.

UNIVERSITY OF WOLLONGONG

COPYRIGHT WARNING

You may print or download ONE copy of this document for the purpose of your own research or study. The University does not authorise you to copy, communicate or otherwise make available electronically to any other person any copyright material contained on this site. You are reminded of the following:

Copyright owners are entitled to take legal action against persons who infringe their copyright. A reproduction of material that is protected by copyright may be a copyright infringement. A court may impose penalties and award damages in relation to offences and infringements relating to copyright material. Higher penalties may apply, and higher damages may be awarded, for offences and infringements involving the conversion of material into digital or electronic form.

Confronting the challenges of tidal flat conservation: spatial patterns and human impacts in a Marine Protected Area in southern NSW, Australia.

A thesis submitted in fulfilment of the requirements for the award of the degree

DOCTOR OF PHILOSOPHY

from

UNIVERSITY OF WOLLONGONG

By

Pia Carmen Winberg, Bachelor of Science (Honours)

INSTITUTE FOR CONSERVATION BIOLOGY

SCHOOL OF BIOLOGICAL SCIENCES

2008

CERTIFICATION

I, Pia Carmen Winberg, declare that this thesis, submitted in partial fulfilment of the requirements for the award of Doctor of Philosophy, in the Institute for Conservation Biology, School of Biological Sciences, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution. All work conducted for this dissertation was conducted under the NSW Marine Parks Permit JBMP 2004/018 Research Authority 2003/011 and the NSW DPI Research Permit P03/0062.

Pia Winberg

14th April 2008.

DEDICATION

I dedicate this thesis to people that make my life most meaningful, my daughters Saskia and Felicia and my lifetime partner Anders.

I also want to dedicate my efforts to the memory of my sister, Eva Maria, for whom I will try to make the most of my time here on this wonderful planet.

TABLE OF CONTENTS

TABLE OF CONTENTS	I
LIST OF FIGURES	V
LIST OF TABLES	XIII
LIST OF PLATES	XVI
ABSTRACT:	XVIII
ACKNOWLEDGEMENTS	XX
CHAPTER 1 - GENERAL INTRODUCTION	1
1.1.1. Why Conservation?	2
1.1.2. The challenges	3
1.2. KEY THEMES OF RESEARCH ON ESTUARINE, TIDAL FLAT ASSEMBLAGES	5
1.2.1. Spatial patterns of Biodiversity	6
1.2.2. Structuring Processes	7
1.2.3. Human impacts	12
1.3. MARINE PROTECTED AREAS – GLOBAL AND LOCAL PERSPECTIVES	13
1.3.1. Objectives of Marine Protected Areas	14
1.3.2. Challenges specific to the establishment and maintenance of MPAs	15
1.3.3. Measured outcomes from MPAs	18
1.3.4. Marine Protected Areas in NSW, Australia	18
1.4. AIMS OF THE STUDY	20
CHAPTER 2 - GENERAL METHODS	23
2.1. DESCRIPTION OF STUDY LOCATION	24
2.2. SAMPLING METHODS – PILOT STUDY	27
CHAPTED 4	24

THE IMPORTANCE OF SPATIAL SCALE FOR THE CONSERVATION OF TIDAL FLAT MACROBENTHOS: A EXAMPLE FROM NEW SOUTH WALES, AUSTRALIA. WINBERG, P. C., T. P. LYNCH, A. MURRAY, A.	
JONES, AND A. R. DAVIS. 2007. BIOLOGICAL CONSERVATION 134: 310-320	ŕ
3.1. Introduction	32
3.1. Methods	35
3.1.2. Study sites	35
3.1.2. Sampling design	37
3.1.2. Analysis of data	38
3.3. Results	40
3.3.1. Estuaries	43
3.3.1. Sites	43
3.3.1. Smaller scale variation	46
3.3. DISCUSSION	47
CHAPTER 4 - ECOLOGICAL EFFECTS OF EXCLUDING BAIT HARVESTIN	G FROM A
TIDAL FLAT: A BEYOND BACI ASSESSMENT OF A MARINE PROTECTED	AREA55
4.2. Methods	59
4.2.1. Location	59
4.2.2. Sampling design	60
4.2.3. Analysis of data	63
4.3. Results	70
4.3.1. Multivariate analysis	70
4.3.2. Univariate analysis	76
4.3.3. Impacts on targeted species – Trypaea australiensis	83
4.3.4. Effects on sediment characteristics	86

4.4. Discussion	87
4.4.1 Assemblage effects	88
7.7.1 Assemblage ejjecis.	
4.4.2 Non-target taxa effects	88
4.4.3 Targeted species	91
4.4.4 Sediment effects	93
4.4.5. Conclusions and Planning and Management considerations for MPAs	94
CHAPTER 5 - ANALYSIS OF MULTIVARIATE AND UNIVARIATE DATA FOR IM	PACT
STUDIES	97
5.1. EXTENDING ASYMMETRICAL ANALYSIS OF VARIANCE IN BEYOND BACI TO BETTER DET	ECT
ENVIRONMENTAL IMPACTS	98
5.5.1. Introduction	98
5.1.2. Methods	100
5.1.3. Case study results	111
5.1.3. Discussion	115
5.2 Maximising bang for your buck: effects of taxonomic resolution, data	
TRANSFORMATION, AND THE USE OF ASSEMBLAGE SUB-SETS FOR DETECTING IMPACTS IN TID	AL FLATS
	117
5.2.1. Introduction	117
5.2.2. Methods	121
5.2.3. Results	130
5.2.4. Discussion	139
CHAPTER 6 - DISCUSSION	147
6.1. GENERAL FINDINGS AND CONSISTENCY WITH OTHER STUDIES	148
6.2. DIRECT IMPLICATIONS FOR MANAGEMENT	150

6.3. POTENTIAL IMPLICATIONS OF FINDINGS	152
6.3.1. Structuring processes	153
6.4. FUTURE DIRECTIONS FOR ECOLOGICAL AND MPA RESEARCH ON TIDAL FLATS	162
REFERENCES	169
APPENDIX I – TIDAL FLAT INVERTEBRATE IDENTIFICATION SHEET (PHOT	
ILLUSTRATIONS)	I
APPENDIX II – QUANTITATIVE DATA	XXIX

List of Figures

Figu	re 1-1. Schematic diagram illustrating a range of structuring relationships between
	organisms and environmental variables that occur in tidal flat habitat. This is not
	the limit of processes and relationships which extend beyond the boundaries of
	tidal flat, and linkages may be mono or bi-directional in effects. The diagram is an
	extension from Snelgrove (1997)
Figu	re 2-1. Map of the extent of unvegetated tidal flat in the Currambene Creek
	location, including an area of intertidal seagrass (Zostera capricorni). The circles
	indicate different densities of feeding craters. 25
Figu	re 2-2. Map of the extent of unvegetated tidal flat in the Currambene Creek
	location, including an area of intertidal seagrass (Zostera capricorni). The blue
	shades represent different tidal heights at six hourly (app.) intervals from high
	(light) to low (dark) tide.
Figu	re 2-3. The average dry weight of sediment retrieved using 1-4 consecutive pumps
	with the bait suction pump, compared to sediment retrieved using a core 150mm
	diameter and 250mm deep. Standard error bars shown
Figu	re 2-4. The average number of T. australiensis specimens and the size frequency
	distribution in each of the methods using 4 bait harvesting pumps or a core30
Figu	re 2-5. The average number of other faunal invertebrates retained using the 4 bait
	harvest pump versus the coring method
Figu	re 3-1 Study locations at three estuaries in the Bateman's Bioregion of NSW.

Australia. The first tidal flat upstream from the estuary mouth was the location
studied, and the general sampling design is illustrated for the Currambene Creek
tidal flat. Three spatial scales were examined: plots (20m), sites (100s of m) and
estuaries (<30km)
Figure 3-2. Species accumulation per sample curves for each of the tidal flats in each of
the three estuaries Currambene Creek, Sussex Inlet and Narrawallee Inlet 42
Figure 3-3. Summary of ANOVA and PERMANOVA results. (a) MDS plots of site
averages using presence/absence multivariate data (beta diversity). (b) Abundance,
Taxonomic Richness and Shannon 'H Diversity means in each of the estuaries.
Standard error bars shown. (c) Magnitude of effects estimates of the different
spatial scale contributions to the overall assemblage variation in all parameters44
Figure 3-4 . MDS plot comparing the composition of macrobenthic assemblages and
relative abundances of taxa at sites. Symbols indicate sites 1-6 in each of the three
locations. The sites measuring 20m in diameter are 100s of metres apart, while
each point represents a 2m plot of 3 replicate cores
Figure 4-1. Location of the three tidal flats, in three different estuaries, on the southern
NSW coast of Australia. The Currambene Creek tidal flat (black star) was
protected in a no-take Marine Protected Area after the first year of sampling
(Impact site), while Sussex Inlet and Narrawallee Inlet (black circles), the control
sites were not protected from bait pumping during the three year study59
Figure 4-2: List of all taxa identified (grouped by phylum or class), and their average
abundance per core in Currambene Creek tidal flat before (C2002) and After

(C2003, C2004) protection in the Jervis Marine Park sanctuary zone (SD bars
S	hown)71
Figure	e 4-3: Second stage MDS plot of resemblance matrices comparing (a) multivariate
a	bundance and composition correlations (Spearman) (untransformed data), and (b)
c	compositional correlation (presence-absence data) from each of the three tidal flats,
(Currambene Creek (C2002 – C2004), Sussex Inlet (S2002 – S2004) and
N	Narrawallee Inlet (N2002 – N2004)
Figuro	e 4-4: Cumulative dominance curves for each year of sampling from the three tidal
f	lats in Currambene Creek (C02 – 03), Sussex Inlet (S02 – 03) and Narrawallee
I	nlet (N02 – 03)74
Figure	e 4-5: Monte Carlo probability P(MC) values for pairwise comparisons of sites
t	between the year before and each of the following two years (2003 and 2004) after
r	no-take zoning. P(MC) are the multivariate equivalent to probability (p) values
υ	sed in univariate tests when three replicates are used. Currambene Creek (C1-6:
b	plack diamonds) is the no-take zone and the control tidal flats (S1-6 and N1-6:
e	empty circles and squares) are shown
Figure	e 4-6: Taxa indicating an increase in abundance in the protected tidal flat
(Currambene Creek (C) compared to control tidal flats (S and N) as shown in Table
4	-4. The changes at individual sites within Currambene Creek are also shown (C1-
(C6). Symbols are denoted at the top of the graph and standard error bars are
S	hown 80

Figure 4-7: Taxa indicating an decrease in abundance in the protected tidal flat
Currambene Creek (C) compared to control tidal flats (S and N) as shown in Table
4-4. The changes at individual sites within Currambene Creek are also shown (C1-
C6). Symbols are denoted at the top of the graph and standard error bars are
shown81
Figure 4-8: Taxa indicating changes in ecological community measures in the protected
tidal flat Currambene Creek (C) Currambene Creek (C) compared to control tidal
flats (S and N) as shown in Table 4-4. The changes at individual sites within
Currambene Creek are also shown (C1-C6). Symbols are denoted at the top of the
graph and standard error bars are shown
Figure 4-9: The percentage length frequency distribution for <i>T. australiensis</i>
populations sampled with a suction pump at each of the tidal flats (C =
Currambene Creek, $S = Sussex$ Inlet, $N = Narrawallee$ Inlet) before (2003 -
hatched) and after (2003-2004) the no-take protection zoning in C (light grey
shade). Sample size ≅ 100 in each year and tidal flat
Figure 4-10: The standard deviation of the size distribution frequency of <i>T. australiensis</i>
in all tidal flats (C = Currambene Creek, S = Sussex Inlet, N = Narrawallee Inlet)
before (dark grey) and after (light grey) no-take protection of Currambene Creek.
Figure 4-11: The ratio of females:males in each tidal flat (C = Currambene Creek, S =
Sussex Inlet, N = Narrawallee Inlet) before (dark grey) and after (light grey) no-
take protection of Currambene Creek

Figure 4-12: Percentage silt and clay content of sediments in (a) each of the tidal flats
(C = Currambene Creek, S = Sussex Inlet, N = Narrawallee Inlet) before (dark
grey) and after (light grey) no-take protection of Currambene Creek, and (b) in
each of the sites in Currambene Creek before and after no-take protection8
Figure 5-1. Spatial asymmetry is accommodated by partitioning the Location sums of
squares into Control sites (C1 & C2) and comparing them to the Impact site (I)
sums of squares. The Impact, indicated with an arrow, occurs in a temporally
balanced design, Before (B1 & B2) and After (A1 and A2). The interaction factor
of interest is CvsI x BvsA. In this example there is also a nested temporal factor
that has the interactions CvsI x Time(B) and CvsI x Time(A)10
Figure 5-2. Spatial asymmetry is accommodated by partitioning the Location Sums of
Squares into Control sites (C1 & C2) versus the Impact site (I). To balance the two
years of After data against one year of Before data, two tests are done using each
of the two years of after data separately. Thus the two tests of interaction are (a)
CvsI x BvsA1 and (b) CvsI x BvsA2. The time of impact is indicated with an
arrow
Figure 5-3. Spatial asymmetry is accommodated by partitioning the Sums of Squares for
into Control sites (C1 & C2) versus Impact (I), and temporal asymmetry is
similarly accommodated by partitioning sums of squares for years into After (A1
& A2) versus Before (B). Thus the test for interaction uses the full data set and is
CvsI x BvsA. The time of impact is indicated with an arrow
Figure 5-4: Sampling and analysis designs: (a) symmetrical Years (3) and Locations (3)

(b) symmetrical Years (3) and asymmetrical Location (2 Control versus 1 Impact);
(c) asymmetrical Years (1 Before versus 2 After) and asymmetrical Location (2
Control versus 1 Impact). Letters indicate fixed factors and numbers random
factors in (a), while (b) and (c) use B = Before, A = After, C = Control sites, I =
Impact site. This illustration technique follows the logic of Benedetti-Cecchi
(2001)

Figure 5-5. Mean species richness in all sites within each estuary measured in 2002 (Before), 2003 and 2004 (After). Sites C1-6 are from the no-take (Impact) tidal flat in Currambene Creek, while sites S1-6 and N1-6 are from the Control tidal flats in Sussex Inlet and Narrawallee Inlet respectively. Standard error bars are shown. 114

Figure 5-6. A schematic diagram based on the logic of Warwick and Clarke (2001) but extended to a third matrix (or second Spearman Rank correlation matrix) to compare the relative effects of data selections, aggregations and transformations on the sensitivity to detect an impact on the assemblage. C, S and N respresent the three locations Currambene Creek, Sussex and Narrawallee Inlets respectively. 129

Figure 5-8. Second stage MDS plots of Spearman	rank correlation coefficients for each
of the abundant species (10%, 20%, 50%, co	ommon 4) and taxonomic resolution
((a) raw/species, genus, family, class/order, j	phyla (b) raw/species, genus, family)
data set similarity matrices, including the for	ur transformations (square root, fourth
root, log(x+1) and presence/absence) for each	h data set

Figure 5-11: Comparison between selected data matrices from Fig. 5-10, comparing the sensitivity of PERMANOVA analysis (p(MC)) to detect an impact in relation to declining Spearman rank correlation with the full original data matrix. The selected data matrices use the following manipulations of the raw, untransformed species

data (r(0)): the four most abundant species untransformed (a4(0), family)untransformed (f(0)), the square root of species that contribute to at least 50% of abundance in samples a3(1), the square root of a4(0) (a4(1)), untransformed class/order (o(0)), fourth root phyla (p(2)), square root raw species data (r(1)), and presence-absence of raw species data (r(4)). The interaction testing for an impact, Years x Control vs. Impact, is presented for two scales; sites (Years x Sites(CvI) and estuaries (Ye x CvsI). Figure 5-12: Comparison of the sensitivity of 7 data manipulations, selected from Fig. 5-10, to detect a change in macrofaunal assemblages at a no-take site (C) compared to control sites (S and N), from the year before no-take zoning (2002) and the following 2 years. The MDS plots show Spearman rank correlations between the 9 beyond BACI structured sets of data. The MDS plot labels are described in Table 5-5. Figure 6-1. some scenarios of potential opposing effects of epibenthic predation on the

List of Tables

Table	e 3-1. Taxa ranked by mean abundance per sample core in each location. Standar	d
Ċ	deviation (SD) and percentage contribution to overall abundance (%) are also	
S	shown. The Phyla or Class to which taxa belong are identified in column Ph. Wi	th
t	the following key: A = amphipoda, B = bivalvia, C = crustacea, F = fish, G =	
٤	gastropoda, I = isopoda, N = nemertea, O = oligochaete. Total values for each	
1	location are presented at the bottom of the table	.41

- Table 3-2. Summaries of PERMANOVA and ANOVA results comparing beta diversity, mean abundance, taxonomic richness and Shannon Diversity (H'). ω^2 (variance components) and % values indicate the proportional contribution of each factor (weighting) to the total variation. P(MC) are Monte Carlo probability values calculated by PERMANOVA. Est = estuary or location, Si = sites, Pl = plots......45
- Table 4-2: The full univariate asymmetrical ANOVA model based on four analyses of variance using different components of the full data set (All, After, Control and After/Control data). The analyses provided the sources of variation (sums of squares) which were used to calculate unknown variation sources for the interactions of interest, that is, to test for effects of no-take zoning on the tidal flat in Currambene Creek (highlighted). F values for the factors of interest used denominator mean squares from factors in order of sequence identified in the F vs.

Table 5-1. Representation of the quantities of sums of squares for interactions for main and nested factors for (a) the full data set (b) after data only, (c) control data only, and (d) after control data only. The calculations in the right hand column provide a full asymmetric †interaction factor represented by the bold outlined sources of sums of squares. This is an extension to the asymmetrical ANOVA, previously

Table 5-4. Asymmetrical analysis of variance calculated from 4 symmetrical ANOVAS

(a – d) using sections of and a full data set of species richness. The factors of interest for extension of the asymmetrical analysis to include a BvsA component are highlighted in blue. Mean square denominators used for F tests are are highlighted in yellow, and factors with an asterisk* are tested with a 2-tail F test.

112
Table 5-5: The suite of treatments used on a raw data set; selectively choosing sub-
groups of common taxa, reducing taxonomic resolution, and increasing the severity
of data transformation. Annotations for the different data sets used in Figures 5-7
are combinations of letters and that are given in parentheses in front of
*(transformations)
Table 5-6: The five different degrees of taxonomic resolution used as data
manipulations to compare the similarity of measured biological patterns123
Table 5-7: The estimated time taken to identify a specimen to different taxonomic levels
(resolution) by taxonomists at the Australian Museum, and the relative number of
specimens (selection) for all taxa, versus taxa that contribute at least 10, 20 or 50%
of abundance, and the four most common and abundant species (a4)133
List of plates
Plate 1. Bioturbation and traces in the tidal flat sediments at low tide (Photos 2-3: F.

Clements). Traces in photos from left to right include an imprint from

Platycephalus sp., naticidae trails and polychaete mounds; a stingray imprint

ABSTRACT:

One of the solutions that has been advocated to reduce anthropogenic impacts in the marine environment, is the concept of a global representative network of Marine Protected Areas (MPAs). The concept seeks to address both conservation and natural resource (eg. fisheries) management, and in Australia, the introduction of MPAs is guided by comprehensive, adequate and representative (CAR) principles. At a local scale however, we face the challenge of identifying areas that collectively fulfil the goals of MPAs when we don't have enough ecological information. This is due to in part to limited knowledge, but is also a result of poor translation of knowledge into the applied realm of management. Consequently, effective MPAs are difficult to plan and balance against diverse stakeholder needs in a political climate. Therefore, it is recognised that ecological science must play an integral part in the development of effective MPAs. In this study, I used MPA zoning in NSW, Australia, as a large scale experiment, to test the effect of no-take zone protection in tidal flat habitat, and also to assess whether the conservation management decisions achieved the MPA goal of representativeness for tidal flat habitat. As bait-harvesting practices for the crustacean Trypaea australiensis (callinassidae) would cease following the zoning of a marine protected area, I sought to address four key aims. First, to describe relevant spatial patterns of tidal flat biodiversity, to assess the representativeness of the tidal flat in a bioregional context, to determine what the impact of bait harvesting was as a structuring process, and finally to determine the effectiveness of no-take zoning for tidal flat habitat and the potential for recovery of the assemblage.

I used a hierarchy of spatially nested scales to sample and test the spatial patterns of tidal flat faunal assemblages, and to determine if the macrofaunal diversity of the protected tidal flat was representative of other tidal flats in the bioregion.

This study documents the first recovery trajectory for tidal flat assemblages in a marine protected area. There was an increase in abundance and homogeneity of smaller, less mobile, suspension and deposit feeding species. In contrast, some of the more mobile, predatory and or scavenging species decreased in abundance. This assemblage shift has the potential for further trophic or functional effects beyond the boundaries of the tidal flat, which are discussed, and thus provides important guidance for future research.

I also found that macrofaunal assemblages were patchily distributed, being most heterogeneous at the scale of 100s m within the tidal flat. For planning and management this implies that whole habitat is required in no-take zones, in order to encompass the full range of macrofaunal diversity in the habitat.

In addition to the key findings, the methods used in this study extended asymmetrical ANOVA to incorporate temporally and spatially asymmetrical factors simultaneously. This extension increases the power and thereby the sensitivity of univariate analysis, to detect environmental change for MPA or impact studies. In addition, data manipulations (taxonomic resolution, assemblage sub-sets and data transformations) demonstrated some dramatic effects on the interpretation of biological pattern.

This study demonstrate the opportunity of using MPA management decisions as a basis on which to test ecological predictions, as well as provide outcomes that can be applied to adaptive planning and management for MPA goals.

ACKNOWLEDGEMENTS

I am totally indebted to the guidance of my primary supervisor, Andy Davis, who has shown me how to balance seriousness with not so seriousness and drink proper coffee. Of importance was your guidance through discussions on a broad range of issues and your generosity with time, but primarily you got me to the point. Thank you also for your belief in that I could achieve this goal and your flexibility in understanding when I was constantly dragged off course with new ideas or sideline projects.

I would also like to express my enormous gratitude to my co-supervisor, Alan Jones at the Australian Museum, whose guidance on important issues was essential to my research; and equally to Anna Murray who provided patient guidance in teaching me about the fascinating world of invertebrates (thank you also for enjoyable food and wine in the big smoke). Thank you to the Australian Museum for providing this support.

Of special significance to this project was the in kind and financial support provided by the Jervis Bay Marine Park. I would particularly like to thank the staff both old and new; Tim, Fran, Leigh, Mark, Robyn, Sue, Ozzie, Julian and Graham. Tim set me on a path of digging in the mud and provided some valuable time and enjoyable moments. In turn I recruited Fran to the mud and I hope to enjoy your wonderful company in future mud projects. Julian was instrumental in saving my frozen samples during a black-out (thus fulfilling the technical glitch requirement of a PhD project). You've taught me what I know about boats Mark and Ozzie (not much but don't take it personally), and thank you to Leigh for providing me with extra-curricula research opportunities.

Further thanks go to staff at the University of Wollongong who provided advice and resources for the project. Thank you Ken Russell at the School of Mathematics and Applied Statistics, Jeff Wright and Mari Dwarte at the School of Biological Sciences, and John Marthick and Brian Jones at GeoSciences.

Other scientific advice was received gratefully from numerous sources including Tom Trinski, Roger Springthorpe and Jim Lowry at the Australian Museum, Graham Edgar (University of Tasmania), Alan Jordan and Rodney James (NSW Marine Parks Authority), Marti J, Anderson (University of Auckland), Bob Clarke (Plymouth Marine Laboratories), Terry Hughes (James Cook University), Alistair Robertson (University of Western Australia), Tony Underwood (Sydney University) and Hugh Possingham (Queensland University).

Fieldworkers Penny, Barbara, Sally and Alex let me spread the joy of mud to others in the world, and made field days much more enjoyable. Especially thanks to Penny for friendship, inspiration and support, and to Alex for hours in the lab.

Further financial support was gratefully received from the Joyce Vickery Research Fund of the Linnean Society of NSW. Other friendly people and places helped along the way; Barry Russell at Shoalhaven City Council and Darryl Halls (LPI) for GIS base station data, Booderee National Park and the Bay of Plenty and Public Transport Union holiday parks for access to field sites.

Finally, thanks to my daughters who have had a PhD candidate as a mother for most of their lives, and who adopted the quirky art of putting worms in jars. Together with the man of my dreams, Anders, you have got me through this milestone – thank you