

This file is part of the following work:

**Vermeiren, Peter Elisa Juliaan (2012) *A landscape level understanding of habitat associations to integrate intertidal crabs into ecosystem models of tropical estuaries*. PhD Thesis, James Cook University.**

Access to this file is available from:

<https://doi.org/10.25903/cm28%2Dfs17>

Copyright © 2012 Peter Elisa Juliaan Vermeiren

The author has certified to JCU that they have made a reasonable effort to gain permission and acknowledge the owners of any third party copyright material included in this document. If you believe that this is not the case, please email

[researchonline@jcu.edu.au](mailto:researchonline@jcu.edu.au)

# ResearchOnline@JCU

This file is part of the following reference:

**Vermeiren, Peter Elisa Juliaan (2012) *A landscape level understanding of habitat associations to integrate intertidal crabs into ecosystem models of tropical estuaries.* PhD thesis, James Cook University.**

Access to this file is available from:

<http://researchonline.jcu.edu.au/40217/>

*The author has certified to JCU that they have made a reasonable effort to gain permission and acknowledge the owner of any third party copyright material included in this document. If you believe that this is not the case, please contact*

*[ResearchOnline@jcu.edu.au](mailto:ResearchOnline@jcu.edu.au) and quote  
<http://researchonline.jcu.edu.au/40217/>*

**A landscape level understanding of habitat associations  
to integrate intertidal crabs into ecosystem models of  
tropical estuaries.**

Thesis submitted by

Vermeiren Peter Elisa Juliaan, BSc. PgDipResMeth.

August 2012

Supervisor: Ass. Prof. Dr. Marcus Sheaves

For the degree of Doctor of Philosophy  
in Tropical Ecology  
within the School of Marine and Tropical Biology  
James Cook University

## Statement of contribution of others

This thesis was made possible due to a substantial financial contribution of the late Christiane De Weirdt, a monthly stipend from the Department of Education, Belgian Government, for the duration of the thesis, a one semester fee contribution from the International Student Centre, James Cook University, and a one semester tuition fee waiver of the School of Marine and Tropical Biology, James Cook University. Project costs were supported by internal research funding from the Graduate Research School, James Cook University.

Supervision was provided by Associate Professor Dr. Marcus Sheaves, who provided guidance in study design, the selection of appropriate data analysis techniques and editorial comments on the content of the thesis. Additional supervision in study design and taxonomic guidance was provided by Adjunct Senior Lecturer Dr. John Collins.

Editorial assistance in terms of thesis content was given by Ross Johnston and Dr. Ronald Baker. Editorial assistance in terms of English language style and spelling were principally provided by Ross Johnston, Dr. Laura Castell, Amanda Buckland and Nina Mclean, with further assistance of John Adams, Ben Davis, Krista Stegemann and Carlo Mattone.

Guidance of interpretation and design of stable isotope analysis studies was provided by Dr. Ronald Baker.

Data-collection was assisted by the contribution of volunteers from the Estuary and Tidal Wetlands Ecosystems Research Group, students from the School of Marine and Tropical Biology and personal friends. In alphabetical order: Amy Foulkes, Ari Stypel, Ashlee Johnson, Ben Davis, Britt Edelman, Christopher Goatley, Cynthia Camacho-Munoz, Deborah Lynn, Donna Hargreaves, Edward Williams, Emma Richmond-Darvill, Falk Ortlieb, Imron Rosyidi, Jade Coase, Jacob Tapp, Janine Sheaves, Jennifer Loder, Jennifer Tanner, Jessica Hacking, Lorena Machado, Louisa Cordingley, Krista Stegemann, Richard Pullinger and Stephanie Johnson.

## Acknowledgments

I would like to thank my parents, Christiane De Weirdt and Wilfried Vermeiren, for their support in making this thesis possible and for giving me their full support in whatever direction I take in life. My wife, Cynthia Camacho-Munoz, I would like to thank for her patience, support and all the things she does to make every day special. Further thanks go to my family and my friends.

I would like to make a special mention of my supervisor, Dr. Marcus Sheaves. I cannot thank him enough for allowing me to pursue research in the direction of my own interests and for making me suffer, but learn, by never giving me a straight answer. Finally, I would like to acknowledge my colleagues from the Estuary and Tidal Wetlands Ecosystems Research Group. They have made the last four years highly educational and fun and have helped me develop myself as a researcher.

## Abstract

The increasing pressures of climate change and urbanization on the ecological functioning and the goods and services provided by tropical estuaries means there is an urgent need for increased understanding of the structure and functioning of important biological components. Intertidal crabs are key components of tropical estuaries and have many characteristics that make them useful model species to study fundamental ecosystem processes. However, most research on their spatial ecology is focused on small scale, habitat-specific interactions, and so lacks applicability at larger within- and across-estuary scales where many fundamental ecosystem processes operate, and where impacts of climate change and urbanization are likely to manifest themselves. To fill this gap, this study aimed to develop enhanced background understanding of intertidal crab spatial ecology needed to allow intertidal crabs to be incorporated into landscape level ecosystem models. A broadly applicable model of intertidal crab habitat associations within the estuarine landscape was developed. This habitat association model focused on the low intertidal zone, between mean low water at spring tide and the lower edge of the mangrove forest, the zone where ecological linkage between intertidal crabs and the estuarine ecosystem is most pronounced.

A distinct intertidal crab assemblage occupied the low intertidal zone. The surface activity pattern of this assemblage was influenced by exposure, temperature and humidity. Consequently, to gain a landscape level understanding of the habitat-associations of intertidal crabs sampling needed to be conducted within a short time frame, while still including high replication. None of the traditionally used methods to sample intertidal crab distribution allows for this type of sampling design. Hence, a new photographic technique capable of high resolution, large-scale spatial distribution mapping was developed.

Maps of intertidal crabs occupying the low intertidal zone of Stuart Creek, North Queensland, Australia, were developed based on the photographic technique. This enabled successful modeling of distinct, temporally stable habitat associations using classification and regression tree models build on independently collected training and test data. Models of these habitat associations were strongly supported by sensitivity testing,

with high sensitivity and low percentages of false positives, in predicting occurrence patterns of six species (*Uca coarctata*, *Uca seismella*, *Macrophthalmus japonicus*, *Metopograpsus latifrons*, *Metopogapsus frontalis* and *Metopograpsus thukuhar*) across eight dry tropical estuaries along 160 km of North Queensland coast. The cumulative model of intertidal crab habitat-associations revealed the low intertidal zone of tropical estuaries as a heterogeneous landscape of taxonomic clusters. Using stable isotope analysis of the dominant species within distinct clusters, unique resource use patterns of intertidal crab assemblages were integrated in the habitat-association model. This final model has the potential to provide a framework for the integration of intertidal crabs in landscape level ecological models of tropical estuaries, and opens the way for new, larger-scale perspectives and investigation of questions regarding niche interactions and the functional roles of the distinct intertidal crab assemblages.

Scientific baselines to support landscape level management are lacking for tropical estuaries. This is largely because much of the diversity of estuarine organisms has not been studied sufficiently to allow spatial distribution patterns to be defined, while others that have been studied show highly variable spatial organization. However, the high predictability of intertidal crab habitat-associations, in combination with their key role in many fundamental ecosystem processes, provides scope to use the understanding gained in this thesis as a scientific baseline to support management of estuaries. Additionally, photographic data underlying the habitat-association model can be collected and analyzed with high accuracy by citizen scientists. Engagement of citizen scientists has the capacity to provide large datasets over broad geographic regions, and to increase the dialogue between science and society. The latter dialogue is crucial as many of the main urban and economic centers of the next few decades will centre on tropical estuaries.

# Table of contents

<b>Statement of contribution of others</b>	<b>p. ii</b>
<b>Acknowledgments</b>	<b>p. iii</b>
<b>Abstract</b>	<b>p. iv</b>
<b>Table of contents</b>	<b>p. vi</b>
<b>List of tables</b>	<b>p. x</b>
<b>List of figures</b>	<b>p. xii</b>
<b>Chapter 1: Intertidal crab assemblages are key elements in the ecological functioning of tropical estuaries</b>	<b>p. 1</b>
1.1 Introduction	p. 1
1.2 Adaptations of Ocypodoidea and Grapsoidea and their relation to spatial distribution patterns	p. 3
1.3 The need for a landscape scale understanding of spatial distribution patterns of intertidal crabs	p. 7
1.4 Thesis structure	p. 10
<b>Chapter 2: Distinct intertidal crab zonation facilitates targeted estuarine research and management</b>	<b>p. 13</b>
2.1 Introduction	p. 13
2.2 Methods	p. 15
2.2.1 Study areas	p. 15
2.2.2 Sample collection	p. 16
2.2.3 Statistical analysis	p. 16
2.3 Results	p. 17
2.4 Discussion	p. 20



<b>Chapter 3: A photographic technique for rapid assessment of large scale intertidal crab distribution</b>	<b>p. 22</b>
3.1 Introduction	p. 22
3.2 Methods	p. 25
3.2.1 Study site	p. 25
3.2.2 The appropriate distance for photographic sampling	p. 26
3.2.3 Reliability and use of data types extracted from photographic samples	p. 26
3.2.4 Standardization of photographs	p. 27
3.2.5 Comparison of photography with three traditional methods	p. 29
3.3 Results	p. 30
3.3.1 The appropriate distance for photographic sampling	p. 30
3.3.2 Reliability and use of data types extracted from photographic samples	p. 31
3.3.3 Comparison of photography with three traditional methods	p. 33
3.4 Discussion	p. 33
<b>Chapter 4: Temperature changes influence temporal connectivity patterns of mangrove crabs</b>	<b>p. 40</b>
4.1 Introduction	p. 40
4.2 Methods	p. 42
4.2.1 Study area	p. 42
4.2.2 Sample collection	p. 43
4.2.3 Statistical analysis	p. 44
4.3 Results	p. 44
4.4 Discussion	p. 45
<b>Chapter 5: A conceptual model of habitat associations of intertidal crabs in a dry tropical estuary</b>	<b>p. 49</b>
5.1 Introduction	p. 49
5.2 Methods	p. 51
5.2.1 Study location	p. 51

5.2.2 Sample collection	p. 53
5.2.3 Statistical analysis	p. 54
5.3 Results	p. 56
5.3.1 <i>U. coarctata</i>	p. 56
5.3.2 <i>U. seismella</i>	p. 58
5.3.3 <i>M. frontalis</i>	p. 59
5.3.4 <i>M. latifrons</i>	p. 60
5.3.5 Overlap in spatial patterns	p. 61
5.4 Discussion	p. 62
<b>Chapter 6: Converting the conceptual model to an ecological model of intertidal crab habitat associations applicable across estuaries</b>	<b>p. 67</b>
6.1 Introduction	p. 67
6.2 Methods	p. 69
6.2.1 Study area	p. 69
6.2.2 Sample collection	p. 70
6.2.3 Statistical analysis	p. 73
6.3 Results	p. 74
6.4 Discussion	p. 81
<b>Chapter 7: Differences in resource use patterns create functional differences across spatially distinct intertidal crabs assemblages</b>	<b>p. 84</b>
7.1 Introduction	p. 84
7.2 Methods	p. 86
7.3 Results	p. 88
7.4 Discussion	p. 92
<b>Chapter 8: Progressing from ecological knowledge to a management baseline with the aid of citizen scientists</b>	<b>p. 94</b>
8.1 Introduction	p. 94
8.2 Accuracy of data collection and analysis	p. 96
8.3 Conclusion	p. 98

<b>Chapter 9: A new landscape level understanding regarding the structure and functioning of intertidal crabs in tropical estuaries</b>	<b>p. 100</b>
9.1 Introduction	p. 100
9.2 Mechanisms underlying spatial distribution patterns within and across estuaries	p. 101
9.3 Implications of spatial distribution patterns within and across estuaries for the ecological role of intertidal crabs	p. 104
9.4 Remarks on the further development of the ecological model	p. 108
<b>Bibliography</b>	<b>p. 109</b>
<b>Appendix 1: ID-sheet for common crabs of the low intertidal zone</b>	<b>p. 129</b>
<b>Appendix 2: Surface activity patterns of intertidal crabs</b>	<b>p. 130</b>
<b>Appendix 3: Additional details of the CART models of habitat-association of intertidal crabs in Stuart Creek (chapter 5)</b>	<b>p. 133</b>
A3.1 Details on the CART model of <i>U. coarctata</i>	p. 133
A3.2 Details on the CART models of <i>M. frontalis</i>	p. 135
A3.3 Details on the CART models of <i>M. latifrons</i>	p. 139
<b>Appendix 4: Additional details of the CART models of habitat-association of intertidal crabs in the landscape level ecological model (chapter 6)</b>	<b>p. 140</b>
A4.4 Details on the CART model of <i>U. coarctata</i>	p. 140
A4.2 Details on the CART model of <i>U. seismella</i>	p. 142
A4.3 Details on the CART model of <i>M. frontalis</i>	p. 143
<b>Electronic appendix: Examples of photographs collected with the photographic method</b>	<b>CD</b>

## List of tables

<b>Table 1.1</b>	Scope of peer reviewed field studies on spatial distribution or habitat associations of intertidal crabs (Weis and Weis, 2004, studied coastal mangroves, Barnes, 1967, studied 3 coastal mangroves)	p. 4
<b>Table 2.1</b>	Taxonomic overview of the species sampled with hand catch in this study	p.17
<b>Table 3.1</b>	Comparison of the five traditional methods and the new photographic method to sample intertidal crabs	p. 23
<b>Table 3.2</b>	Similarities in the number of individuals recorded by the experienced observer and each of the inexperienced observers	p. 31
<b>Table 3.3</b>	Similarities in the number of individuals observed by during the first observation and each of the subsequent observations by the experienced observer	p. 31
<b>Table 3.4</b>	Comparison of data collection and analysis strengths and weaknesses of photography, hand catch, visual observation and pitfall trapping. (The experienced observer took 15 minutes and each of the inexperienced observers took 1hour to analyse the whole subset of 20 photo quadrats for relative occurrence)	p. 35
<b>Table 3.5</b>	Error sources in photographic sampling	p. 38
<b>Table 4.1</b>	Partial correlation coefficients of the different activity patterns with temperature and humidity	p. 45
<b>Table 5.1</b>	The average percentage of sites ( $\pm$ SE) per species that overlap into the predicted high occurrence cluster of <i>U. coarctata</i> and sites predicted to be occupied by <i>U. seismella</i> , <i>M. frontalis</i> and <i>M. latifrons</i>	p. 62
<b>Table 6.1</b>	Sampling times and estuaries, including components and the number of sites sampled within them	p. 71
<b>Table 6.2</b>	Sensitivity recorded for individual species habitat-association models in the test systems. (-) Indicates systems that could not be tested for that species, species are: <i>U. c.</i> : <i>Uca coarctata</i> , <i>U.</i>	p. 78

s.: *Uca seismella*, M. j.: *Macrophthalmus japonicus*, M. f.:  
*Metopograpsus frontalis*, M. l.: *Metopograpsus latifrons* and M.  
t.: *Metopograpsus thukuhar*

<b>Table 6.3</b>	Percentages of false positives recorded for individual species habitat-association models in the test systems. (-) Indicates systems that could not be tested for that species. species are: <i>U. c.</i> : <i>Uca coarctata</i> , <i>U. s.</i> : <i>Uca seismella</i> , M. j.: <i>Macrophthalmus japonicus</i> , M. f.: <i>Metopograpsus frontalis</i> , M. l.: <i>Metopograpsus latifrons</i> and M. t.: <i>Metopograpsus thukuhar</i>	p. 79
<b>Table 6.4</b>	Percentages of overlap in predicted spatial distributions of species across all test systems, species are: <i>U. c.</i> : <i>Uca coarctata</i> , <i>U. s.</i> : <i>Uca seismella</i> , M. j.: <i>Macrophthalmus japonicus</i> , M. f.: <i>Metopograpsus frontalis</i> , M. l.: <i>Metopograpsus latifrons</i> and M. t.: <i>Metopograpsus thukuhar</i>	p. 80
<b>Table A3.1</b>	Misclassification errors of the within-site CART models of <i>U. coarctata</i>	p.134
<b>Table A4.1</b>	Percentage sensitivity and false positives observed in the model and test systems for the two models of <i>U. coarctata</i> .	p. 142
<b>Table A4.2</b>	Percentage sensitivity and false positives in the model and test estuaries for the two models of occurrence of <i>M. frontalis</i>	p. 144

## List of figures

<b>Figure 1.1</b>	Conceptual diagram depicting the relationship between the thesis chapters	p. 12
<b>Figure 2.1</b>	Overview of the study area with specific sampling locations	p. 15
<b>Figure 2.2</b>	CART of mean standardized relative abundance ( $\pm$ SE) of species (recorded with hand catch) produced a three leaf three based on intertidal zones (systematic error explained: 45%)	p. 18
<b>Figure 2.3</b>	Two-dimensional nMDS representing the similarity between sites and the species composition across the habitat landscape based on relative abundances of species (A, Stress = 0.16.) and presence of species (B, Stress = 0.11). Data from particular habitats are enclosed by convex hulls (colored polygons).	p. 19
<b>Figure 3.1</b>	Location of the study site: Ross River, Townsville, Australia	p. 25
<b>Figure 3.2</b>	Standardization of photographs taken on banks with different bank angles to match the area of the standard photo quadrat	p. 28
<b>Figure 3.3</b>	Cumulative percentage of observations in different distance classes in which crabs responded to the observer (including standard error, based on 60 observations)	p. 30
<b>Figure 3.4</b>	Relative contributions (%) of species to the total sample for absolute abundance, relative abundance and presence/absence photographs, hand catch and visual observations	p. 32
<b>Figure 4.1</b>	Location of sampling areas in Bohle River and Ross River, North Queensland, Australia	p. 43
<b>Figure 5.1</b>	Location of Stuart creek with indication of study section	p. 52
<b>Figure 5.2</b>	Example of the stratified sampling design used, with indication of upper and lower parts within areas as a basis for site selection	p. 53
<b>Figure 5.3</b>	Mean percentage within-estuary occurrence ( $\pm$ SE) of species across the study period	p. 56
<b>Figure 5.4</b>	CART model for within-site occurrence of <i>U. coarctata</i> , including the number of sites (N) and mean contribution (C) of within-site occurrences per cluster relative to the sum of the within-site	p. 57

	occurrence across all clusters, as observed in the training data	
<b>Figure 5.5</b>	Percentage contribution of the relative occurrence of <i>U. coarctata</i> in each cluster relative to the total relative occurrence across clusters per trip ( $\pm$ SE) in the model and test trips	p. 57
<b>Figure 5.6</b>	CART model of presence/absence of <i>U. seismella</i> with indication of the number of sites (N) and the contribution (C) of <i>U. seismella</i> presences in each group relative to the total number of presences recorded across all groups, as observed in the training data	p. 58
<b>Figure 5.7</b>	Percentage contribution of the presence of <i>U. seismella</i> in each group relative to the total number of presences across all clusters per trip ( $\pm$ SE) for the training data and test trips	p. 59
<b>Figure 5.8</b>	Percentage contribution of the presence of <i>M. frontalis</i> in each group relative to the total number of presences across all clusters per trip ( $\pm$ SE) for the training data and test trips	p. 60
<b>Figure 5.9</b>	Percentage contribution of the presence of <i>M. latifrons</i> in each group relative to the total number of presences across all clusters per trip ( $\pm$ SE) for the training data and test trips	p. 61
<b>Figure 5.10</b>	Conceptual model of the patterns of spatial organization of intertidal crab assemblages within a tropical estuary based on the predictions for the four individual species models. Rectangles are presence/absence models and the triangle is based on the relative occurrence model of <i>U. coarctata</i> . Species are organized along a spatial niche axis, which in this case is strongly driven by changes in structural complexity	p. 64
<b>Figure 6.1</b>	Location of estuaries studied	p. 70
<b>Figure 6.2</b>	Schematic overview of the sampling design used, with indication estuarine components and the areas, selected based on changes in vegetation, within the low intertidal zone of these components	p. 72

<b>Figure 6.3</b>	CART models of habitat-association for individual species, based on presence-absence within site data, with indication of the number of sites (N) within each group of sites and the average percentage (C) of occurrences of each species within each group across the model estuaries	p. 77
<b>Figure 6.4</b>	An ecological model of broad habitats of intertidal crabs occupying the low intertidal zone, based on individual species habitat-association models	p. 81
<b>Figure 7.1</b>	Location of study system (Bohle River) with different sections, and location of the reference site for isotopic signatures of primary producers (Ross River).	p. 87
<b>Figure 7.2</b>	Mean and minimum and maximum range of isotopic values recorded for intertidal crabs species in Bohle River estuary, and minimum and maximum range isotopic values (grey boxes) of primary producers in the Ross River estuary (modified from Abrantes and Sheaves, 2008)	p. 90
<b>Figure 7.3</b>	$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values recorded for individuals of four crab species across locations in three sections of the Bohle River estuary (each sample comprises 3 individual crabs)	p. 91
<b>Figure 8.1</b>	An easy to use inclinometer to measure bank angles	p. 98
<b>Figure 9.1</b>	Example of the process of information layering, using the ecological model of habitat associations as the framework	p. 107
<b>Figure A2.1</b>	Patterns in abundance of intertidal crabs and in temperature and humidity levels over time after emergence of their habitat. All values were standardized relative to the lowest value recorded and expressed as a percentage relative to the highest value recorded for crab abundance, temperature and humidity. Data on crab abundance were visualized with a distance weighted least squares smoothing function	p. 131
<b>Figure A3.1</b>	Percentage contribution of the relative occurrence of <i>U. coarctata</i> in each cluster relative to the total relative occurrence across all clusters per trip ( $\pm$ SE) in the training and test trips	p. 134



<b>Figure A3.2</b>	CART model presence/absence of <i>M. frontalis</i> with indication of number of sites (N) and contribution (C) of the presence of <i>M. frontalis</i> in each group relative to the total number of presences across all clusters per trip, as observed in the training data	p. 136
<b>Figure A3.3</b>	Percentage contribution of the presence of <i>M. frontalis</i> in each group relative to the total number of presences across all groups per trip ( $\pm$ SE) for the training and test trips	p. 137
<b>Figure A3.4</b>	CART model for relative occurrence of <i>M. frontalis</i> , including the number of sites (N) and mean contribution (C) of relative occurrence per cluster relative to the total relative occurrence across all clusters, as observed in the training data	p. 138
<b>Figure A3.5</b>	Percentage contribution of the relative occurrence of <i>M. frontalis</i> in each cluster relative to the total relative occurrence across all clusters per trip ( $\pm$ SE) in the training data and test trips	p. 138
<b>Figure A3.6</b>	CART model for presence/absence of <i>M. latifrons</i> , including the number of sites (N) and the contribution (C) of the presence of <i>M. latifrons</i> in each group relative to the total number of presences across all groups per trip, as observed in the training data. 2L indicates results for the two leaf model, 3L, indicates results for the three leaf model	p. 139
<b>Figure A4.1</b>	CART models for predicted presence of <i>U. coarctata</i> with indication of number of sites (N) and the observed contribution, expressed in percentage, of occupied sites in each group relative to the total number of occupied sites in the model systems	p. 141

# **Chapter 1: Intertidal crab assemblages are key elements in the ecological functioning of tropical estuaries**

## **1.1 Introduction**

Tropical estuaries are highly productive systems providing a variety of goods and services to human populations. Examples include the provision of food, construction materials and medicines, the protection against coastal erosion, the trapping of pollutants and the provision of a nursery for many commercially important fish species (Alongi, 2002). Accordingly, tropical estuaries are among the economically highest valued ecosystems (Costanza et al., 1997, Ronnback, 1999, 2001). However, the ecological functioning and the goods and services provided by tropical estuaries are endangered by increasing urbanization and climate change (Duke et al., 2007, Lovelock and Ellison, 2007, Alongi, 2008). Large areas of tropical estuaries are rapidly disappearing (Valiela et al., 2001) and the condition of remaining areas is degrading (Alongi, 2002, Duke et al., 2007). Additionally, the development of many of the main urban and economic centers of the next few decades is expected to centre on tropical estuaries, further augmenting the pressure on tropical estuaries (Seto, 2011). Consequently, accurate ecological models are critical to understand the functioning of tropical estuaries and ultimately to serve as a framework for sustainable management of these ecosystems.

Intertidal crabs are a key component of tropical estuaries and have many characteristics making them potentially useful model species to study the ecological functioning of these systems. The superfamilies of Ocypodoidea (particularly the family Ocypodidae) and Grapsoidea (particularly the families Grapsidae and Sesarmidae) dominate the intertidal crab fauna (Lee, 2008, Nagelkerken et al., 2008). Both families are highly abundant, intimately linked to many biological components and involved in key ecological processes through their roles in trophic transfer and ecosystem engineering (Angsupanich and Aksornkoae, 1996, Apel and Tuerkay, 1999, Amaral et al., 2009). For example, they influence sediment composition (Botto and Iribarne, 2000, Escarpa et al., 2004), productivity (Koch and Wolff, 2002, Werry and Lee, 2005), vegetation structure (Bosire et

al., 2005), faunal composition (Dye and Lasiak, 1986, Botto et al., 2000) and energy fluxes (Wolff et al., 2000). Consequently, shifts in intertidal crab assemblages are likely to influence the wider estuarine community and ecosystem functioning. Additionally, adult intertidal crabs generally have restricted home ranges (Cannicci et al., 1996a, Layne et al., 2003, Guest et al., 2006, Zeil and Hemmi, 2006, Dauvin et al., 2010) and short life spans (Nobbs and McGuinness, 1999, Hilty and Merenlender, 2000), hence, their effects on the estuarine ecosystem can be investigated on local scales and short timeframes.

Crabs occur throughout the intertidal zone of tropical estuaries, but the assemblage within the low intertidal zone, the area between mean low water at spring tide and the edge of the mangrove forest, offers greatest potential for the development of an easy to use ecological model that is linked to many ecosystem processes. The connectivity between crabs and the estuarine ecosystem is most pronounced in the low intertidal zone because regular tidal inundation enables interactions between the resident crab fauna and transient estuarine components. For example, aquatic and terrestrial fauna such as aquatic crabs, fish (Cannicci et al., 1996a, Sheaves and Molony, 2000) and birds (Botto et al., 2000) move in and out of low intertidal banks during different tidal periods (Sheaves, 2005), and nutrients and various other materials are deposited or exported with the tides (Bouillon et al., 2008). Additionally, intertidal crabs that inhabit the low intertidal zone are easy to observe and identify because they are exposed during ebb tide (Eshky et al., 1995) and many of them have easy recognizable color patterns (Nobbs and McGuinness, 1999, Appendix 1).

Despite their potential as key elements of ecological processes in tropical estuaries, the integration of intertidal crabs in a broad ecological context has been hampered by a lack of a widely applicable understanding of their spatial distribution within and across estuarine landscapes. In fact, many studies on spatial distribution patterns of intertidal crabs focus on small, within-site or within-transect scales and have limited replication across sites and scales (Table 1.1). Furthermore, despite the heterogeneous environmental landscape available on low intertidal banks (Lee, 2008), most studies on intertidal crab spatial ecology focus on one or a limited set of environmental areas. For example, in the low intertidal zone, most studies are centered on flat, featureless mud banks that are easily accessible (Lee, 2008, Vergamini and Mantelatto, 2008, Takeda, 2010, but see Lim and

Heng, 2007). Consequently, extrapolation of the results of these studies is restricted because of the constrained understanding of their applicability to other environments. Similarly, the few system-wide studies conducted usually focus on large-scale gradients, for example across the intertidal (Koch et al., 2005), along salinity gradients (Ness, 1972) or along broad upstream-downstream divisions (Ravichandran et al., 2007) and fail to consider the smaller scale environmental heterogeneity in physical factors along which these gradients operate within the estuarine intertidal landscape. Nonetheless, physical heterogeneity plays an important role in structuring the spatial distribution of sessile root epibiotic communities at 1m to 1km scales within estuarine landscapes in Belize (Fransworth and Ellison, 1996). Consequently, the difference in morphological, behavioral and physiological adaptations between Ocypodoidea and Grapsoidea could influence their spatial distribution across the low intertidal zone of tropical estuaries. Therefore, the next paragraphs will give an overview of the main differences between adaptations of intertidal Ocypodoidea and Grapsoidea that could influence their spatial distribution.

## **1.2 Adaptations of Ocypodoidea and Grapsoidea and their relation to spatial distribution patterns**

The low intertidal zone is a highly dynamic environment where temperature and humidity fluctuate widely (Micheli et al., 1991, Wolfrath, 1993, Eshky et al., 1995). These fluctuations can affect fundamental life-sustaining processes, such as thermoregulation, respiration and food uptake of intertidal crabs (Maitland, 1990) and are thus likely to influence spatial distribution patterns of intertidal crabs. For example, most Ocypodidae (Ocypodoidea) have the capacity to construct burrows in which temperatures and humidity levels are more constant than at the sediment surface (Eshky et al., 1995). By contrast, Grapsidae and Sesarmidae (Grapsoidea) often rely on shallow burrow networks (Kristensen, 2008) or find shelter among roots, leaves or natural crevices (Warren, 1990). Additionally, tree dwelling Grapsidae generally remain among tree roots, branches or trunks and often occupy specific crevices (Cannicci 1996a, 1999, Sivasothi, 2000). Consequently, the type of shelter utilized by the crabs and the degree of protection provided by the environment against surrounding conditions, for example via the type of

structural elements or the amount of canopy overhang, could influence spatial distribution patterns of intertidal crabs.

**Table 1.1** Scope of peer reviewed field studies on spatial distribution or habitat associations of intertidal crabs (Weis and Weis, 2004, studied coastal mangroves, Barnes, 1967, studied 3 coastal mangroves)

<b>Author</b>	<b>No. of estuaries</b>	<b>No. of sites or transects</b>	<b>No. of species</b>
Takeda, 2010	1	1	2
Vergamini and Mantelatto, 2008	1	1	1
Ravichandran et al., 2007	1	5	46
Lim and Heng, 2007	1	1	1
Arruda-Bezerra and Matthews-Cascon, 2006	1	8	4
Koch et al., 2005	1	1	4
Weis and Weis, 2004	1	2	4
Ashton et al., 2003	1	2	31
Nobbs, 2003	1	1	3
Sirajul et al., 2003	1	Unknown	15
Dahdouh-Guebas et al., 2002	2	5	7
Hartnoll et al., 2002	4	8	2
Cannicci et al., 1999	1	1	2
Cannicci et al., 1998	1	1	1
Cannicci et al., 1996a	1	1	1
Mouton and Felder, 1996	1	6	2
Eshky et al., 1995	1	2	2
Mclvor and Smith, 1995	2	8	16
Frusher et al., 1994	1	5	4
Ewa-Oboho, 1993	1	7	2
Bertness and Miller, 1984	1	1	1
Jones and Simons, 1982	1	17	2
Frith and Brunenmeister, 1980	1	1	5
Seiple, 1979	2	16	2
Icely and Jones, 1978	1	5	4
Jones, 1976	1	13	5
Sasekumar, 1974	2	3	30
Miller and Mauer, 1973	3	20	2
Hartnoll, 1973	1	1	1
Warner, 1969	1	2	10
Barnes, 1967	5	5	5
Teal, 1958	1	8	6
Snelling, 1958	1	24	23

The degree of structural complexity of the environment can further influence spatial distribution patterns via its interaction with predator avoidance strategies. The burrowing behavior of Ocypodidae, in combination with restricted home ranges (Zeil and Hemmi, 2006) and highly developed burrow orientation mechanisms (Zeil, 1998) provide a protection strategy against predators in habitats where little structure for shelter is available. Additionally, the position of their eyes on long stalks allows them to maintain a low posture on the sediment surface, while still being able to perceive other organisms (Zeil and Hemmi, 2006). In fact, the morphology of their eyes is specifically adapted to discern between predators in the upper part of their field of view and social signals of other crabs in the lower part. This division of the field of view is most effective in flat, low structure habitats where the distribution of predators and co-specifics is organized along a vertical axis (Zeil and Hemmi, 2006). By contrast, the position of the eyes of Grapsidae and Sesarmidae at extreme ends of their carapace allows for a well developed stereoscopic vision (Zeil and Hemmi, 2006). This allows Grapsidae and Sesarmidae to gauge distances and to move efficiently through habitats characterized by high structural complexity.

Ocypodoidea and Grapsioidea rely on different methods of communication which could influence their spatial distribution across environments with different structural complexity. Ocypodidae utilize visual communication strategies, such as claw waving and changes in body posture (Zeil and Hemmi, 2006, How et al., 2008). The utilization of visual communication could strongly restrict spatial distribution patterns to areas with little structural complexity, particularly for small Ocypodidae with highly developed waving displays, such as *U. seismella* (von Hagen, 1993). Visual signals are likely to be used by Grapsoidea as well. For example, color patterns of Sesarmidae are used as visual signals to attract mates (Boon et al., 2009). However, Sesarmidae also poses specialized morphological features which are used for sound reception and production, such as grooved patterns on the claws (Boon et al., 2009). These morphological adaptations allow for social interactions in environments irrespective of the structural complexity. Some Ocypodidae are reported to produce sound (Popper et al., 2001). However, given their large claws and species specific waving displays (Perez et al., 2012), visual communication is likely to remain the dominant method for their communication strategy.

Most intertidal crabs have restricted home ranges and must thus obtain nutrition in close proximity to their shelters (Cannicci et al., 1996a, Zeil and Hemmi, 2006). Additionally, species that migrate across the habitat landscape generally do so in search of food (Murai et al., 1982, Koga, 1995, Gherardi et al., 2002). Consequently the distribution of food sources could exert a substantial influence on the spatial distribution of many intertidal crabs. Ocypodidae usually feed on sediment microorganisms, including bacteria, microalgae and fungi, and detritus (Hsieh et al., 2002, Meziane et al., 2002). These are abundantly available across the low intertidal zone, due to high levels of organic matter deposition and high light levels (Bouillon et al., 2002). However, the sediment feeding mechanism utilized by Ocypodidae to extract these food sources from the sediment is highly specialized and differs between species (Icely and Jones, 1978, Lim and Kalpana, 2011). In fact, many studies comparing the spatial distribution of individual Ocypodidae have found differences in sediment properties such as dominant sediment grain size, sediment organic matter content or sediment water content (Weis and Weis, 2004, Koch et al., 2005, Arruda Bezerra et al., 2006, Lim and Kalpana, 2011), corresponding to an influence of sediment feeding mechanisms on spatial distribution patterns.

Grapsoidae are frequently considered leaf feeders and their distribution is often related to mangrove tree species (Dahdouh-Guehas, 1999). However, Grapsoidae are a diverse group and a high dependence on leaves as a main source of nutrition is likely only found in a few species, particularly within the family of Sesamididae (Dahdouh-Guehas, 1999). By contrast, *Metapograpsus* spp. (Grapsidae) primarily feed on macroalgae which predominantly grow on hard substrata such as logs, roots or rocks (Poon et al., 2010, Nordhaus et al., 2011). Hence, their distribution is likely more related to the availability of hard substratum. Additionally, the algal diet of *Metapograpsus* spp. is often supplemented with other products, including MPB's and meat (Lee, 1998, Poon et al., 2010, Nordhaus et al., 2011). This opportunistic feeding is also supported for many other Grapsidae (Giddins et al. 1986, Micheli 1993, Skov and Hartnoll 2002). Consequently, the relation between Grapsidae and mangrove tree species is likely more complex than just a dependence on mangrove leaves as food sources. In particular, the relation might be contributed to the physical structure or the indirect provision of different sources of nutrition by various mangrove tree species (Lee and Kwok 2002).

### **1.3 The need for a landscape scale understanding of spatial distribution patterns of intertidal crabs**

All of the differences in morphological, behavioral and physiological adaptations discussed in the previous paragraphs suggest that different species of intertidal crabs could be tailored to occupy different environments. In fact, relationships have been successfully established between the spatial distribution of individual intertidal crab species and specific environmental factors, most notably sediment organic matter content, sediment grain size, salinity, dominant vegetation types and tidal height (Nobbs, 2003, Weis and Weis, 2004, Koch et al., 2005). Such strong associations between crab species and the environment indicate that the pattern of spatial distribution of intertidal crab assemblages could for a large part be driven by spatial niche assemblages, because niche theory, when applied to spatial distribution patterns, poses that the spatial niche occupied by a species is determined by the interactions of this species with the biotic and abiotic environment (Potts et al., 2004). However, the strength of associations between crabs and the environment and of niche assemblages as a mechanism structuring spatial distribution patterns has not been assessed within and across landscape scales. A landscape scale conceives estuaries as spatially continuous mosaic which encompasses the potential habitat diversity within an estuarine environment typical for a certain geographical region, in which a habitat is outlined by a spatially distinct population (Fausch 2002). This definition of landscape level outlines the smallest spatial unit "habitat" in an ecological sense, thereby setting an ecologically meaningful scale at which patterns can be understood. Additionally, the definition allows for the inclusion of smaller "individual mosaic" scale studies. Finally, it defines the overall, large "geographical" scale in which the understanding gained can be applied. An understanding of the patterns of spatial distribution and the mechanisms driving it across landscape scales is crucial to understand the stability and predictability of spatial distribution patterns and to appreciate the transferability of knowledge regarding spatial ecology of intertidal crabs across estuaries, all of which allows for an improved integration of intertidal crabs into ecological models of fundamental estuarine processes.



The ecological understanding that can be gained from studying the habitat-associations of intertidal crabs at landscape scales could provide the necessary scientific baseline that is lacking in many estuarine management and monitoring programs (Cox et al., 2005, Moss et al., 2005). Despite the increasing pressure on tropical estuaries (Duke et al., 2007, Lovelock and Ellison, 2007, Alongi, 2008, Seto, 2011), the ability to make comprehensive management decisions is hampered by the lack of appropriate ecological baselines of the spatial distribution patterns of many tropical estuarine organisms. An ecological baseline provides an understanding of the organism's ecology and the methods to apply this understanding in the collection of concrete data for research or monitoring applications. The spatial extent of these ecological baselines should be large enough to include the system-wide scale at which the effects of urbanization and climate change are likely to operate, while the resolution should be sufficiently fine to include the habitat scale at which faunal patterns are organized (Fausch et al., 2002, Lee et al., 2006). Additionally, ecological baselines need to be pertinent across estuaries to allow the development of broadly applicable management strategies (Sheaves and Johnston, 2010). Finally, to facilitate transparency of ecological data and enhance the integration of these data in the wider socio-economic debates surrounding holistic management of ecosystem goods and services (Glaser, 2003, Burger et al., 2008, Raymond et al., 2009), the baselines should rely on simple, easy to use methods and protocols. However, such widely applicable, landscape level baselines of spatial distribution patterns are unavailable for many tropical estuarine organisms. In fact, a large part of the diversity of estuarine organisms has not been studied sufficiently to allow spatial distribution patterns to be formulated (Nagelkerken et al., 2008) while others show highly variable spatial organizations across estuaries (Sheaves and Johnston, 2010). Given their wide distribution and key role in many estuarine processes, intertidal crabs could provide the scientific baseline to support estuarine management.

This thesis aims to develop the large scale ecological understanding needed to incorporate intertidal crabs in landscape level ecosystem models and management strategies of tropical estuaries. In particular the thesis will:

1. Establish simple, easy to use sampling protocols for the collection of data regarding habitat associations of intertidal crabs occupying the low intertidal zone at a landscape level.

2. Develop a preliminary model of habitat-associations of intertidal crabs within the low intertidal zone and test the applicability of this model across estuaries.
3. Link the resulting habitat-association model to the ecological functioning of tropical estuaries, particularly focusing on the trophic interactions of intertidal crabs.
4. Assess the applicability of the ecological baseline for broad scale management of tropical estuaries.

In order to achieve these aims, this thesis is structured in the following chapters:

## **1.4 Thesis structure** (Fig. 1.1)

### **Chapter 1: Intertidal crab assemblages are key elements in the ecological functioning of tropical estuaries**

This chapter outlines the large ecological role of intertidal crabs occupying the low intertidal zone of tropical estuaries and highlights the lack of a landscape level understanding of their spatial distribution. p. 1

### **Chapter 2: Distinct intertidal crab zonation facilitates targeted estuarine research and management**

This chapter assesses the existence and taxonomic identity of distinct crab assemblages occupying the habitat landscape of the low intertidal zone versus other intertidal zones. p. 10

### **Chapter 3: A photographic technique for rapid assessment of large scale intertidal crab distribution.**

This chapter investigates key issues underpinning the development of a new photographic method for high replication sampling of spatial distribution patterns of crabs within and across the low intertidal zone of tropical estuaries. p. 19

### **Chapter 4: Temperature changes influence temporal connectivity patterns of mangrove crabs.**

This chapter studies the patterns and drivers of surface activity of intertidal crabs to be able to account for them in sampling and modeling of intertidal crab assemblages using photographic methods. p. 36

### **Chapter 5: A conceptual model of habitat associations of intertidal crabs in a dry tropical estuary.**

This chapter develops and tests a simple conceptual model of habitat associations of different species of crabs within the low intertidal zone of one estuary. p. 45

**Chapter 6: Converting the conceptual model to an ecological model of intertidal crab habitat associations applicable across estuaries.**

In this chapter, the simple conceptual model of intertidal crab habitat associations constructed in Chapter 5 is further developed and tested to produce a broadly applicable ecological model of spatial organization of intertidal crab assemblages within and among estuaries. p. 63

**Chapter 7: Differences in resource use patterns create functional differences across spatially distinct intertidal crabs assemblages.**

This chapter looks into the functional implications of the distinct spatial distribution patterns of intertidal crabs by analyzing the dietary resource use patterns of the main intertidal crab species that were modeled in Chapter 6. p. 81

**Chapter 8: Progressing from ecological knowledge to a management baseline with the aid of citizen scientists.**

In this chapter, a first step is made to integrate the understanding of spatial distribution patterns gained in this thesis into management applications, by testing the robustness of the photographic protocols developed in Chapter 3 for use by citizen scientists to collect accurate data to support scientific baselines. p. 90

**Chapter 9: A new landscape level understanding regarding the structure and functioning of intertidal crabs in tropical estuaries.**

In the final chapter, the understanding gained in this thesis regarding spatial distribution patterns of intertidal crabs across the estuarine habitat landscape is deepened by discussing the potential mechanisms underlying the observed distribution patterns and by expanding on their implications for the ecological function of intertidal crabs in the estuarine ecosystem. p. 96

## Site specific understanding

Ch.1: Ecological importance of intertidal crabs

Ch.2: Low intertidal is a distinct fauna

## Need for a new method

Ch.3: Photographic sampling  
=> how to sample

Ch.4: Activity patterns  
=> when to sample

## landscape level understanding

Ch.5: one estuary

Ch.6: Among estuaries



Ch.8: Application of the photographic technique in citizen science

=> collection of large scale data to reinforce and further develop the model

Ch.7: Linking of the landscape model to the rest of the ecosystem



Lower trophic orders

## Discussion

Ch.9: underlying mechanisms and implications for the ecological functioning

**Figure 1.1** Conceptual diagram depicting the relationship between the thesis chapters

## **Chapter 2: Distinct intertidal crab zonation facilitates targeted estuarine research and management**

### **2.1 Introduction**

Climate change and urbanization have variable effects on the proportion and condition of intertidal habitats which, in turn, affect the spatial distribution of organisms occupying these zones (Irmiler et al., 2002). Albeit largely based on old research, the dominant superfamilies of intertidal crabs (Ocypodoidea and Grapsoidea) are generally considered to occupy two distinct intertidal zones (Snelling, 1958, Warner, 1969). In particular: Grapsoidea dominate the high intertidal zone, usually corresponding to the mangrove forest, while Ocypodoidea dominate the low intertidal zone (Snelling, 1958, Warner, 1969). The latter Ocypodoidea zone is further divided in an upper portion, with intertidal banks which are dominated by Ocypodidae, and a lower portion with mudflats, dominated by Macrophthalmidae (Snelling, 1958, Warner, 1969). Considering the unique ecosystem engineering and trophic interactions mediated by intertidal representatives of the two main superfamilies (Kristensen, 2008), changes to the estuarine landscape can affect the type of ecosystem services provided by intertidal crabs within a tropical estuary. Additionally, because this thesis aims to develop an ecological model of habitat associations focused on the low intertidal zone, up to date knowledge on the existence and taxonomic identity of distinct crab zones is necessary to relate this model to the wider intertidal crab community.

Despite the long history of the concept of distinct intertidal crab zones (Snelling, 1958, Warner, 1969), recent quantitative evidence supporting this concept is scarce. Hartnoll et al. (2002) described a gradient in Grapsoidea versus Ocypodoidea biomass in relation to tidal height, while Ravichandran et al. (2007) presents a table of taxonomic zones but does not explain how these taxonomic zones relate to explicit intertidal zones. Additionally, in opposition to the conventional view, Ocypodidae were found across eight transects spanning the intertidal of the Pacoti River, Brazil, where their distribution was more closely related to sediment properties than tidal height (Arruda-Bezerra and Matthews-Cascon, 2006). In fact, spatial distribution patterns of intertidal crabs are

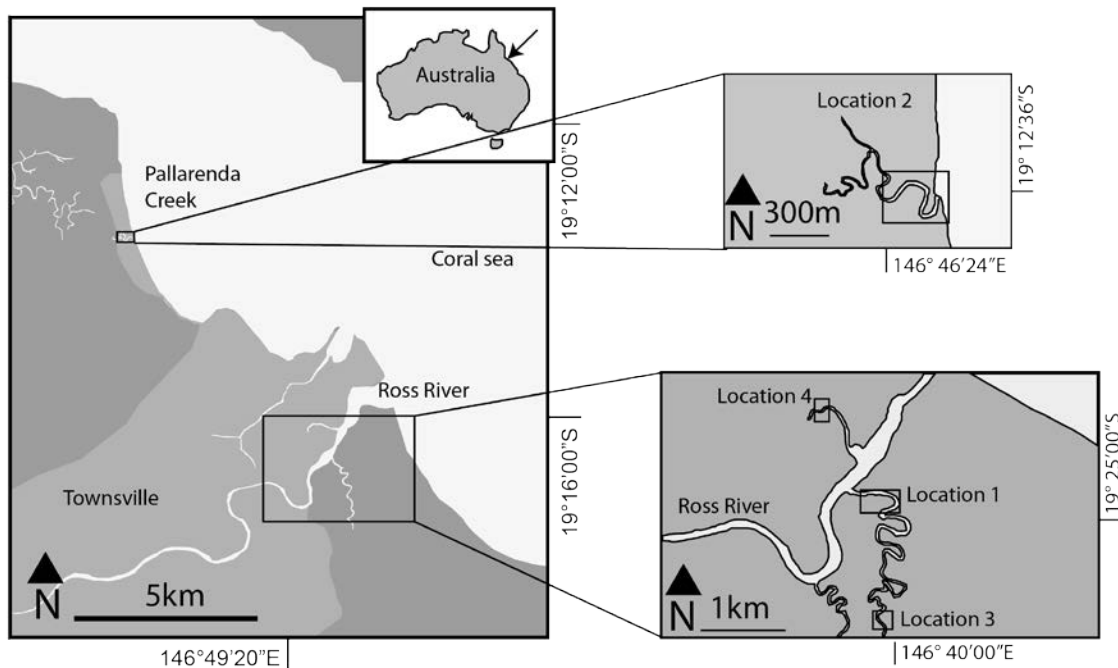
governed by a complex interplay of environmental factors which can vary both in concordance or disparate from intertidal zones (Ashton et al., 2003, Arruda-Bezerra and Matthews-Cascon, 2006). Hence, the existence of distinct intertidal zones with unique taxonomic crab assemblages is still debated and may vary on a situation-specific basis.

The main reason for the lack of a clear understanding of the existence and taxonomic identity of intertidal crab zones can be traced to the constraints of the study designs employed to sample intertidal crabs. Most studies of spatial distribution patterns of intertidal crabs focus on small, site specific scales, with each study generally using its own specific sampling strategy (Ashton et al., 2003, Arruda Bezerra et al., 2006, Vergamini and Mantelatto, 2008). Because of unknown biases in the faunal assemblage sampled with different protocols, comparison of results from these small scale studies is restricted across intertidal zones. Additionally, studies that sample across the intertidal generally only examine a small number of transects and each transect is usually closely matched to the others in terms of the habitats it passes through (Arruda Bezerra et al., 2006). However, because the intertidal of tropical estuaries provides a compound environmental landscape containing a diversity of potential habitats, such sampling designs are likely to underestimate the faunal diversity available within the habitat landscape of tropical estuaries (Lee, 2008). This could skew the current understanding of intertidal crab zones. Hence, a better understanding of the relationships between intertidal crab assemblages sampled at different locations within the intertidal habitat landscape is urgently required. Specifically, this understanding provides the necessary background to place the crab assemblage occupying the low intertidal zone, which is the assemblage studied in this PhD thesis, in context of the whole intertidal crab community. Therefore, this chapter aims to provide an assessment of the existence and taxonomic identity of crab assemblages within the intertidal landscape of tropical estuaries that encompasses different intertidal zones, but also investigates the potential diversity of habitats within zones.

## 2.2 Methods

### 2.2.1 Study areas

Sampling was conducted within four intertidal locations around Townville, North Queensland, Australia ( $19^{\circ}16'00''\text{S}$ ,  $146^{\circ}49'20''\text{E}$ , Fig. 2.1). The habitat landscape within each location was divided into habitats based on their intertidal position (low intertidal bank, medium intertidal forest or high intertidal flat) and the dominant vegetation (*Ceriops* spp., *Rhizophora stylosa*, *Avicennia marina* or no vegetation). The low intertidal bank was defined as the position between the water edge and the area where the sediment surface noticeably change to a slope of less than 10degrees. The area following was divided based on the presence or absence of mangrove trees in medium intertidal forest and high intertidal flat respectively. Sampling was conducted between 17 and 21 May 2011 in area 1 and on 3, 5 and 16 April 2011 in area 2, 3 and 4 respectively, during the ebb tide after the high tide had covered the substratum. Salinities within the estuary channel at the time of sampling were consistently near local sea water salinity of 35 ‰.



**Figure 2.1** Overview of the study area with specific sampling locations



### **2.2.2 Sample collection**

Samples of the intertidal crab fauna within location 1 were collected at three replicate sites within each habitat using hand catch, video sampling and pitfall trapping methods. Additionally, two replicate hand catches within each habitat were conducted within location 2, 3 and 4. Hand catches were conducted for 5 minutes per site with the aid of a shovel to block burrow entrances (Macintosh et al., 2002, Castiglioni and Negreiros-Fransozo, 2005). Video samples were collected using a camera which was mounted on a 2m pole and faced straight down towards the sediment. This allowed continuous, undisturbed observation of a 1m<sup>2</sup> area for two hours. Video samples were analyzed for 1 minute every 15 minutes. The pitfall traps consisted of planting pots, 20cm deep, 17cm wide, with perforations less than 1mm at the bottom to allow drainage. Five pitfall traps were set up in a 4m<sup>2</sup> area per site at low tide on one day and collected at low tide the next day (Skilleter and Warren, 2000, Salgado Kent and McGuinness, 2006). Hand catch data were analyzed for relative abundances of crab species that were active on the sediment surface. In addition, data from video, pitfall and hand catch were combined to give a more complete representation of the crab fauna that is less dependent on the bias of any one method. To allow all methods to have equal input, presence data were used. All captured crabs were identified to the lowest taxonomic level possible (based on the taxonomy presented in Ng et al., 2008) and released after identification.

### **2.2.3 Statistical analysis**

Data were analyzed with non-metric multidimensional scaling (nMDS) and classification and regression tree analysis (CART, De'ath 2002). Relative abundance data were pooled per habitat for each location and row standardized to obtain comparable estimates of crab faunal composition across habitats where hand catch might have variable success rate. Presence data were used without standardization. Data on location, intertidal position and dominant vegetation were used as predictor variables. The similarity in crab faunal composition across habitats, using both relative abundance (across all locations) and presence absence (locations 1 only) data, was visualized on an nMDS plot using a Manhattan distance matrix and single linkage between sites. Species vectors were plotted on the nMDS plot via linear regression of each species unto the dimensions of the nMDS. The size of the species vectors were relative to the coefficient of determination and the direction was determined by the regression coefficients for each dimension of the nMDS.

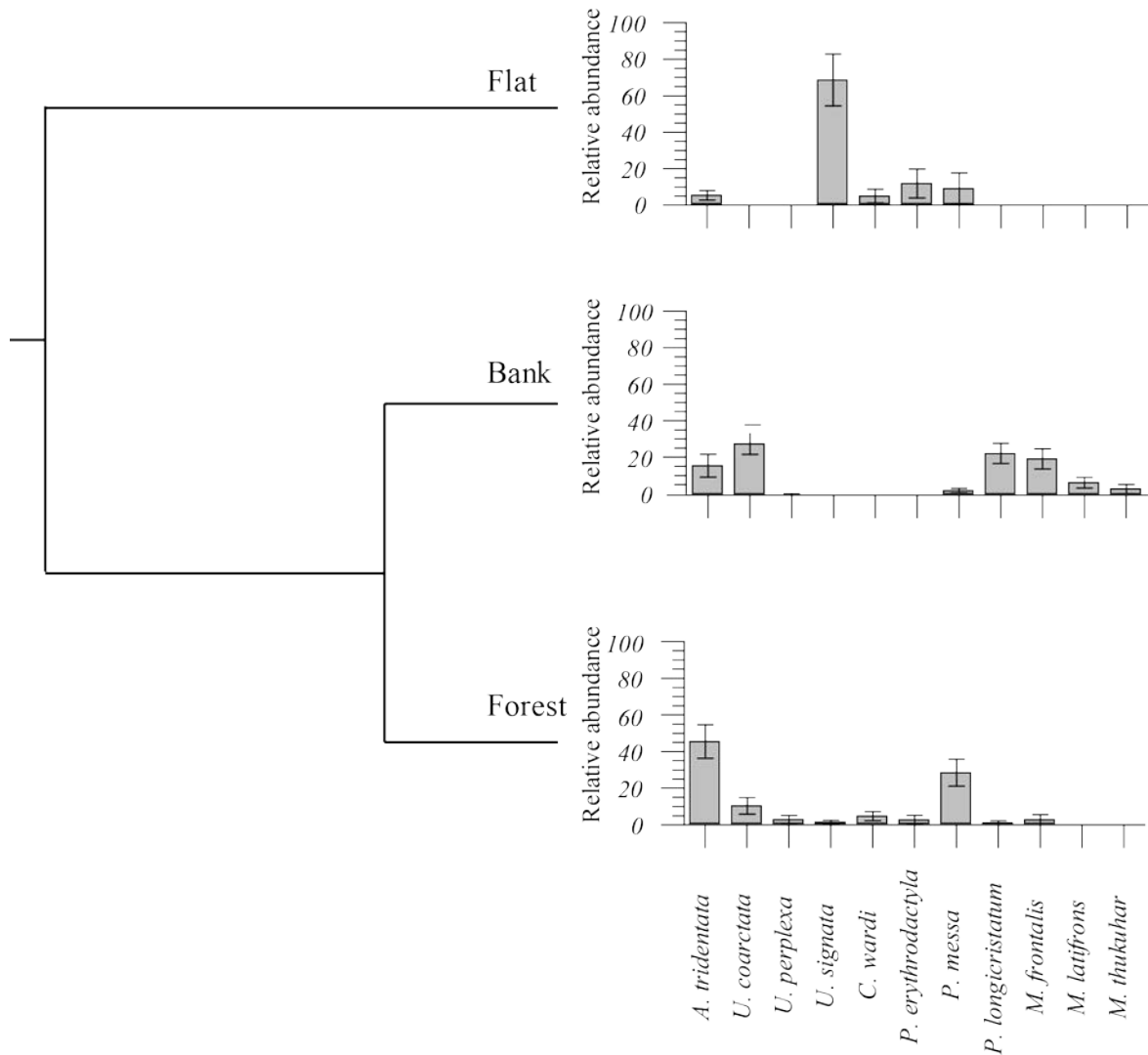
The factors relating to the distinct assemblages of intertidal crabs were further analyzed using CART. CART analyses were run using least squared deviations and pruned via 10-fold cross validation (CV). The smallest tree with a CV cost within 1 standard error of the minimum CV cost was recorded each time, and the most consistent outcome over 50 individual model runs selected.

## 2.3 Results

Distinct assemblages were associated with specific intertidal zones, but these were not simply a function of higher taxonomic identity. Eleven species of intertidal crabs across two families and five subfamilies were recorded in hand catch samples (Table 2.1). CART analysis of the relative abundance data collected in these samples resolved into a three leaf tree in 92% of iterations (Fig. 2.2). This tree identified distinct assemblages based on intertidal zones, each with a mixture of species across different taxonomic groups (Fig. 2.2). First, high intertidal flats, which were dominated by *U. signata*, were separated, then, mid intertidal forests, which were dominated by *A. tridentata* and *P. messa*, were separated from low intertidal banks on which *A. tridentata*, *U. coarctata*, *P. longicristatum* and *M. frontalis* were the dominant species (Fig. 2.2).

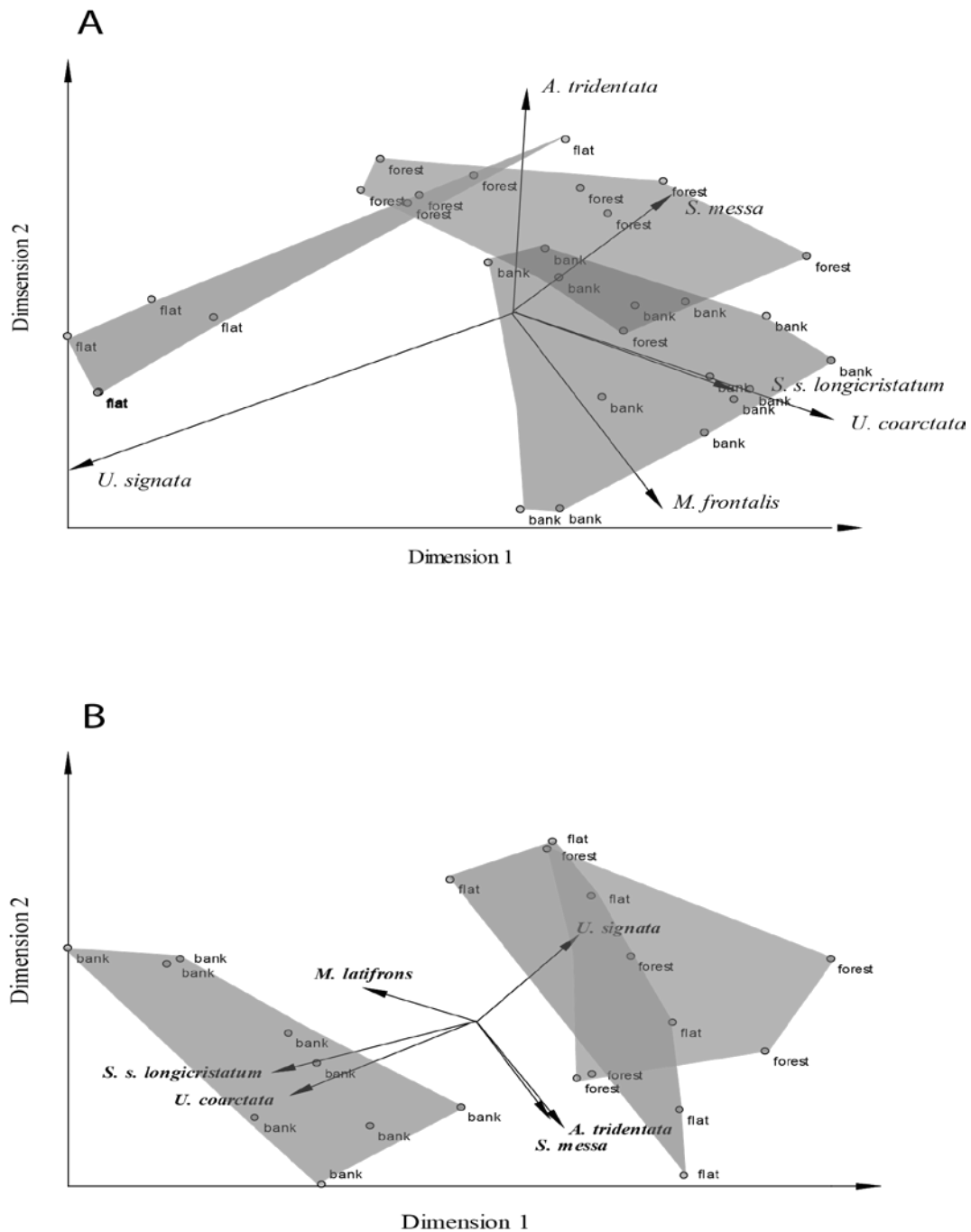
**Table 2.1** Taxonomic overview of the species sampled with hand catch in this study

Superfamily	Family	Species
<b>Ocypodoidea</b>	Macrophthalmidae	<i>A. tridentata</i>
	Ocypodidae	<i>U. coarctata</i>
		<i>U. perplexa</i>
		<i>U. signata</i>
	Camptandriidae	<i>C. wardi</i>
<b>Grapsoidea</b>	Sesarmidae	<i>P. erythroductyla</i>
		<i>P. messa</i>
		<i>P. longicristatum</i>
	Grapsidae	<i>M. frontalis</i>
		<i>M. latifrons</i>
		<i>M. thukuhar</i>



**Figure 2.2** CART of mean standardized relative abundance ( $\pm$ SE) of species (recorded with hand catch) produced a three leaf three based on intertidal zones (systematic error explained: 45%)

Presence data collected with video sampling, hand catch and pitfall trapping did not record any additional species compared to the relative abundance data collected solely with hand catch. Furthermore, the pattern of organization of assemblages in distinct intertidal zones observed in presence data mirrors that detected in relative abundance data (Fig. 2.3 a, b). Because presence data were not influenced by the high abundances of *U. signata* caught on some flats, they provide a clearer visualization of the differences between banks and forests in terms of occurrence.



**Figure 2.3** Two-dimensional nMDS representing the similarity between sites and the species composition across the habitat landscape based on relative abundances of species (A, Stress = 0.16.) and presence of species (B, Stress = 0.11). Data from particular habitats are enclosed by convex hulls (colored polygons)

## 2.4 Discussion

Rather than distinct taxonomic zonation, intertidal zones were distinguished by specific assemblages comprising crabs from different families. Ocypodidae occupied exposed habitats (Zeil and Hemmi, 2006, Kristensen, 2008) found on both low intertidal banks and high intertidal flats, as evidenced by the associations of *U. coarctata* and *U. signata* respectively. However, some low intertidal banks, such as those lined by *R. stylosa*, have high structural complexity which makes them less exposed and potentially more suitable for species of Grapsidae. This could explain the association of *M. latifrons*, which is a root dwelling species (Sivasothi, 2000), with low intertidal banks. Similarly, while many Sesarmidae are found in mid intertidal forests, because they feed on leaf litter which is abundantly available in these forests (Dahdouh-Guebas et al., 2002), some of them such as *Perisesarma longicristatum* and *Parasesarma erythroductyla* in this study, reached higher abundance on low intertidal banks and high intertidal flats respectively, and contributed a large part of the crab abundance at these intertidal positions. These results differ from the previously held concept that intertidal crabs are organized across the intertidal according to family level (Snelling, 1958, Warner, 1969, Hartnoll et al., 2002, Ravichandran et al., 2007). At least part of the reason for this difference is that most previous studies on spatial distribution patterns of intertidal crabs focus on a subsection of habitats within the intertidal habitat landscape (Ashton et al., 2003, Arruda Bezerra et al., 2006, Vergamini and Mantelatto, 2008), so the full diversity of habitats and species within intertidal zones might previously have been underestimated (Lee, 2008).

Despite the absence of distinct higher taxonomic zonation, the existence of specific crab assemblages in different intertidal zones provides an ecologically meaningful division of the intertidal habitat landscape. Both relative abundance data, collected with hand catch, and presence data, collected using a combination of hand catch, pitfall trapping and video recordings, identified distinct faunal assemblages across intertidal zones. This pattern of intertidal zonation is likely a reflection of the unique environments dominating distinct intertidal zones. In fact, intertidal position is related to many of the dominant environmental factors that can affect intertidal crabs across the habitat landscape such as changes in vegetation composition, structural complexity, canopy protection against temperature and

humidity fluctuations, the slope of the surface, sediment organic matter and water content and grain size distribution of the substratum (Dahdouh-Guebas et al., 2002, Koch et al., 2005, Arruda Bezerra et al., 2006, Ravichandran et al., 2007, Lee, 2008). Despite the great distinctions in faunal composition across the intertidal positions, some of the similarities observed might give clues to the factors underlying this pattern. For example, the species composition, as shown by presence-absence data (Fig 2.3A), are more similar between forest and flat than between either of those and the bank. Potentially, factors relating to the tidal height such as inundation frequency and duration or sediment grain size distribution, which are very different on intertidal banks compared to the flat and forest, might have a strong effect in organizing intertidal crab communities across the intertidal. In conclusion, the physiological adaptations of intertidal crabs and the functional interactions they mediate are likely to vary in concordance with these dominant environmental gradients across the intertidal. Consequently ecological study and management applications can be focused on distinct intertidal zones and specialize on the unique characteristics and problems of the crab assemblages within them. Additionally, the potential effects of climate change and urbanization can be visualized and addressed relative to the intertidal levels where their specific impacts will be manifested.

# **Chapter 3: A photographic technique for rapid assessment of large scale intertidal crab distribution**

## **3.1 Introduction**

Crabs often dominate the fauna of the low intertidal zone of tropical estuaries (Nagelkerken, 2008), where they influence a variety of ecological processes via trophic interactions and ecosystem engineering (Bouillon et al., 2002, Escarpa et al., 2004, Bosire et al., 2005, Werry and Lee, 2005, Nordhaus et al., 2006, Mchenga and Tsuchiya, 2008). These influences often extend beyond the low intertidal zone because regular tidal inundation in this zone provides connectivity to both the aquatic and terrestrial component of tropical estuaries (Lee, 2008, Sheaves and Johnston, 2009). This strong connectivity between intertidal crabs and the estuarine ecosystem means that they are closely interlinked to many fundamental ecosystem processes (Amaral et al., 2009). However, a lack of quantified understanding of the spatial distribution of intertidal crabs at a whole-of-estuary scale prevents these crabs from being incorporated in landscape level models of these processes and restricts knowledge of the contribution of intertidal crabs to the ecosystem functioning of tropical estuaries.

One reason for the lack of a landscape level understanding is a divide between the scale and resolution at which spatial distribution patterns are currently investigated. Most studies of spatial distribution patterns of intertidal crabs focus on small, site or transect specific scales with limited replication in other sites or transects (Chapter 1). Despite the high resolution in these studies, their limited replication prevents generalisation of the studied patterns at larger, estuary-wide scales. Alternatively, the few studies that focus on larger, estuary-wide spatial distribution patterns usually lack resolution for finer habitat patchiness (Snelling, 1958, Ness, 1972) and thus fail to represent important variability at this finer scale.

In part, the divide between scale and resolution in which spatial distribution of intertidal crabs is addressed is a function of the methods traditionally employed to sample intertidal crabs. In fact, none of the five traditionally used methods: visual observation, hand catch, pitfall trapping, excavation and burrow counts (Table 3.1), of which the first three are most commonly used (Nobbs and McGuinness, 1999, Jordão and Oliveira, 2003, Salgado Kent and McGuinness, 2006), are appropriate for large scale and high resolution sampling of spatial distribution patterns. For example, excavation and pitfall trapping are labour intensive and consequently cannot achieve a high level of replication (Jordão and Oliveira, 2003). Hand catch is faster, but as with excavation and pitfall trapping, the procedure disturbs soft intertidal sediments, with effects often extending beyond the actual area sampled. As a result, it may be impossible to obtain independent replicates close to an area already sampled and subsequent repeated samples are often biased by the disturbance caused during previous sampling events. The advantage of the three previous techniques is that crabs are physically captured (Salgado Kent and McGuinness, 2006), meaning carapace measurements can be obtained, sex determined and species level identification made.

**Table 3.1** Comparison of the five traditional methods and the new photographic method to sample intertidal crabs

<b>Method</b>	<b>Excavation</b>	<b>Pitfall trapping</b>	<b>Hand catch</b>	<b>Visual observation</b>	<b>Burrow count</b>	<b>Photography</b>
<b>Speed</b>	Slow	Slow	Medium	Medium	Medium	Fast
<b>Destructiveness</b>	High	High	High	Low	Low	Low
<b>Physically obtains crabs?</b>	Yes	Yes	Yes	No	No	No
<b>Ecological knowledge required?</b>	Burrowing behavior	Activity patterns, Mobility	Burrow behavior, Activity patterns	Activity patterns	Burrow behavior	Activity patterns
<b>Applicable in multi-species assemblages?</b>	Yes	Yes (but highly specific)	Yes	Yes	Difficult	Yes

The last two traditional methods, visual observation and burrow count (Skov et al. 2002, Salgado Kent and McGuinness, 2006), do not allow the facility to physically obtain crabs.



Both methods are usually considered rapid techniques (Skov et al. 2002, Jordão and Oliveira, 2003) with the potential to collect highly replicated spatial information. However, visual observation requires use of a quadrat, the installation of which causes crabs to retreat to their burrows, meaning data collection is not possible until the crabs re-emerge (Jordão and Oliveira, 2003, Salgado Kent and McGuinness, 2006). Burrow counts are also time consuming, can be difficult to conduct in structurally complex habitats and are hard to interpret in multispecies assemblages (Lee, 1998, Skov et al. 2002, Jordão and Oliveira, 2003). Thus, although the five traditionally used methods certainly have their use, a new sampling technique is needed to address large-scale, high resolution spatial distribution patterns of intertidal crabs. Photography is one such technique.

Photography has been used extensively to map spatial distribution patterns of a range of organisms at a variety of scales and across different environments (e.g. terrestrial vegetation types: Fensham and Fairfax 2002; intertidal rocky shore communities: Blakeway et al. 2004; marine benthic communities Solan et al. 2003). Its low cost, ease of operation and ability to collect large numbers of replicates quickly make this technique attractive in both research and monitoring situations (Solan et al., 2003, Blakeway et al., 2004). Intertidal crabs are active when the sediment surface is exposed and have restricted home ranges (Zeil and Hemmi, 2006). Additionally, while some species of intertidal crabs can only be identified with the aid of a microscope, many have recognisable, definitive colour patterns (Frusher, 1988). The latter species are likely to be ideal candidates for photographic sampling

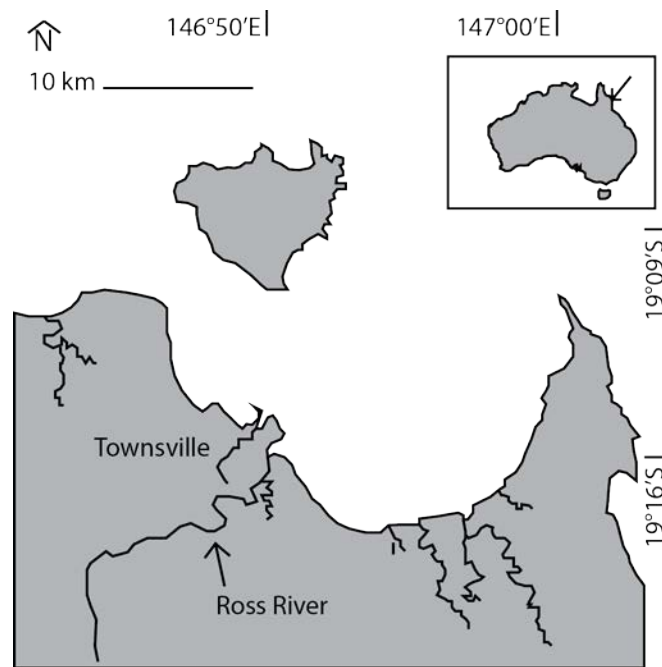
This chapter investigates key issues underpinning the development of a new photographic method for sampling spatial distribution patterns of crabs occupying the low intertidal zone of tropical estuaries. The following issues are considered:

- 1) At what distance can crabs be photographed without affecting their behaviour?
- 2) What type of data can be reliably extracted from photographs, how does each data type perform and which data are appropriate for specific applications?
- 3) What are the biases in samples obtained with photography, in terms of the species composition and species estimates, compared to samples obtained with traditional methods, specifically the three most commonly used: hand catch, pitfall trapping and visual observation.

## 3.2 Methods

### 3.2.1 Study site

The estuary of Ross River, Townsville, Australia ( $19^{\circ}16'25''\text{S}$ ,  $146^{\circ}49'58''\text{E}$ , Fig. 3.1), contains a diverse range of mud banks within the low intertidal zone. These banks can broadly be categorised into four morphologically distinct bank types, each providing a different environment for intertidal crabs. Flat to medium angle banks are lined at their upper extents by mixed *Avicennia marina* and *Rhizophora stylosa* forests which provide structure in the form of pneumatophore and prop roots across the low intertidal zone. Medium angle banks are predominantly bordered by *R. stylosa* with prop roots overhanging into the low intertidal zone. Medium to steep angle banks are dominated by *Ceriops* spp. forest or scrub at their landward edges providing structure in the form of buttress roots at the mid to upper limit of the low intertidal zone. Steep angle banks are bounded by salt couch, *Sporobolus virginicus*, containing some grass clumps at the upper limit of the low intertidal zone. Additional structure in the form of dead timber can be present in all bank types. Banks are flooded twice daily by semi-diurnal tides, with tidal ranges greater than 3m on spring tides.



**Figure 3.1** Location of the study site: Ross River, Townsville, Australia

### ***3.2.2 The appropriate distance for photographic sampling***

For each of the four bank types, the behaviour of 15 different groups of crabs was observed through a camera, while progressively shortening the distance between the observer in a boat and the crabs. The boat was driven straight towards the bank at 3 to 4km/hour, a velocity at which the boat produced no wash and photographs could be taken with ease. Observations started at 20m and the distance at which crabs showed a visible change in behaviour in response to the observer was measured by focussing the camera at that point and reading the distance from the camera focus ring in classes: 0-3, 3-5, 5-10 and 10-20m. Since crabs usually perceive objects in the upper part of their field of view as threats (Zeil and Hemmi, 2006), all observations were conducted while seated. Data were collected during daytime low tide between 13 and 15 April 2011. These were clear, sunny days with daytime low tide between 12am and 1.30pm. The appropriate distance for photographic sampling was determined as the shortest distance between crabs on the bank and an observer in a slow moving boat, at which none of the crabs responded to the observer.

### ***3.2.3 Reliability and use of data types extracted from photographic samples***

Reliability of absolute abundance, relative occurrence and presence/absence data extracted from photographic samples was tested using 120 photographs spread over three replicate sets of 10 for each of the four bank types (examples of photographs can be found in the electronic appendix). Photographic sampling was conducted during ebb tide between 13 and 15 April 2011 from a dinghy at 12m distance from the bank (a distance at which no crabs responded to the observer). Photographs were shot straight towards the bank, because colour patterns of intertidal crabs were most visible and crabs living on the outside layer of overhanging roots were easiest to detect with this camera orientation. Additionally, a handheld 6-megapixel camera with a 200mm zoom lens and a diaphragm opening of F8 was used. With these settings, photo quadrats in which crabs were in focus could be collected on banks of any bank angle. The average bank angle was measured with an inclinometer which is held parallel to the bank, after which a gravitationally directed needle indicates the bank angle  $-90^{\circ}$ . Since the bank angle was measured for each replicate set of 10 photographs, standardised dimensions could be calculated for all photo quadrats to ensure that on average the same total area was sampled in each.

### 3.2.4 Standardization of photographs

Photographs taken of vertical banks were taken as the standard photo quadrat, (110cm wide by 80cm high). The bottom of photographs taken on banks other than vertical was aligned with the bottom of this standard photo quadrat. Subsequently, the standard photo quadrat was tilted under the bank angle, using the bottom as the pivotal axis, and the projection of the standard photo quadrat back onto the photographs calculated (Fig. 3.2). The projected height ( $H_{proj}$ ) can easily be deduced via trigonometry because the photograph that is formed in the camera will always be parallel to the projected standard quadrat, hence creating  $90^\circ$  angles.

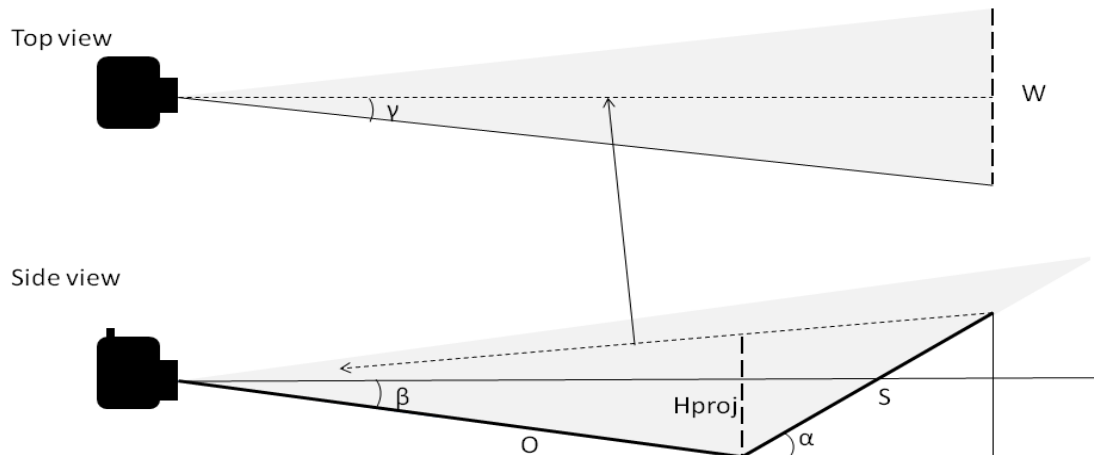
$$H_{proj} = O \sin \beta + O \cos \beta (S \sin \alpha - O \sin \beta) (O \cos \alpha + S \cos \alpha)$$

$S$  is the length of the standard photo quadrat,  $O$  the observer distance,  $\alpha$  the bank angle minus the angle under which the camera is held and  $\beta$  is half the vertical angle of view of the camera. The projected height ( $H_{proj}$ ) divided by the length of the standard photo quadrat gives the fraction of the height of the standard photo quadrat that is included in the observed photo quadrat.

The width of the bank at the top of a standard photo quadrat becomes larger on lower angled banks. The width of the top of the projection ( $W$ ) is given by:

$$W = 2 \tan \gamma \sqrt{(O \cos \beta + S \cos \alpha)^2 + (S \sin \alpha - O \sin \beta)^2}$$

$\gamma$  is half the horizontal angle of view of the camera. Divided by the width of the standard photo quadrat, this gives the fraction of the top of the standard photo quadrat that is included in the observed photo quadrat. Projections were done in  $10^\circ$  classes.



**Figure 3.2** Standardization of photographs taken on banks with different bank angles to match the area of the standard photo quadrat

In the standardised photo quadrats, absolute abundance for each species was obtained by counting the number of individuals of that species within the photo quadrat. Relative occurrence was estimated by dividing each photo quadrat into a grid of twelve equal subsections (3 x 36.7cm horizontal and 4 x 20cm vertical divisions) and counting the number of grid cells occupied by a species. Finally, presence/absence data was obtained by recording the presence of a species in each photo quadrat. Photo quadrats were magnified on the computer allowing visualisation of smaller crabs (until 0.5cm carapace size).

For the first reliability of extraction test, all 120 photographs were analysed, in random order, four separate times by an experienced observer for absolute abundance, relative occurrence and presence/absence. In the second reliability of extraction test, a subset of 20 randomly selected photographs was analysed independently by one experienced observer and three inexperienced observers for relative occurrence and presence/absence. The latter procedure was conducted to assess if this technique can be used for routine monitoring by people without specific knowledge of intertidal crabs. The inexperienced observers had no previous skill identifying crabs, but were provided with photographs of 16 common intertidal crabs (see Appendix 1). The similarities in results obtained with absolute abundance or relative occurrence were compared with correlation.

The similarities in presence/absence data were cross-tabulated in a 2x2 table and the  $\pi$ -square correlations (Siegel and Castellan, 1988) calculated. The  $\pi$ -square correlation provides a measure of relation between variables in two-way frequency tables where the measurements are nominal (in this case presence-absence).

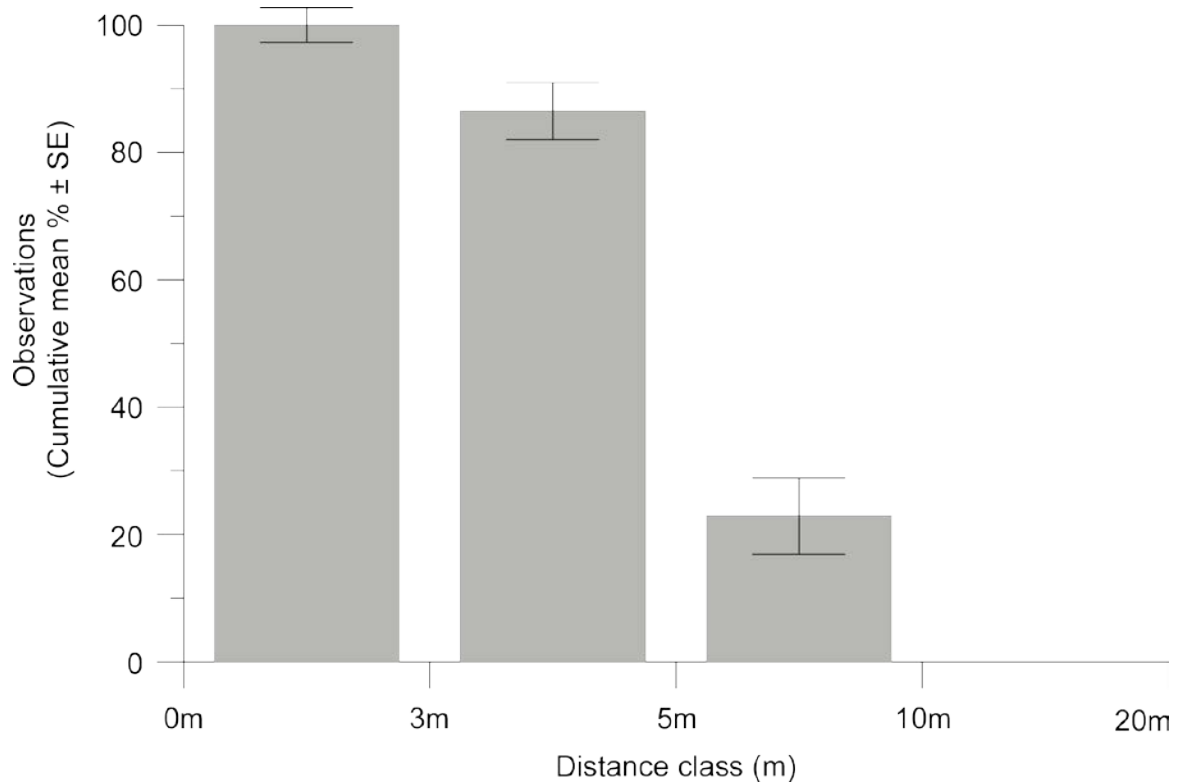
### ***3.2.5 Comparison of photography with three traditional methods***

The bias in species composition and species estimates between the photographic method and three traditional methods was investigated by accompanying each series of ten photographs, collected as described in the previous paragraph, with one visual observation, one hand catch and two pitfall traps. Burrow counts were not conducted because background knowledge on which crab belongs to which burrow is not available. Similarly, the high numbers of roots within the substratum in most sample sites prohibited excavation. However, although each of the three methods has its own biases, together they include a broad cross section of typical crab sampling approaches and should provide a reasonable representation of the relative species composition within sites against which the biases of photography can be assessed. All methods except pitfall trapping were carried out within 1 hour in random order, between 13 and 15 April 2011. Pitfalls were set up at low tide on one day and collected at low tide the next day. Visual observation of a 1m<sup>2</sup> quadrat was done from 1m distance for two minutes after a 15 minutes waiting period to allow the crabs to re-emerge from their shelter (Jordão and Oliveira, 2003, Salgado Kent and McGuinness, 2006). Hand catch, with the aid of a shovel to block burrow entrances and to do rapid excavations of burrows where crabs were observed to escape into, was done for 5 minutes per site (Macintosh et al., 2002, Castiglioni and Negreiros-Fransozo, 2005). The size of the hand catch sites depended on the area that could be covered in 5 minutes, but was generally between 5 and 10m<sup>2</sup>. All crabs were identified to the lowest taxonomic level possible and released after identification. No crabs were caught with the original two pitfalls per site which consisted of planting pots, 20cm deep, 17cm wide, with perforations less than 1mm at the bottom to allow drainage. Therefore, an additional nine sites were sampled on 21 and 22 May 2011 using the same photographic technique and hand catch, but with a more intense pitfall trapping scheme. This consisted of five pitfall traps of the same specifications, in a two by two meter imaginary square per site (Skilleter and Warren, 2000, Salgado Kent and McGuinness, 2006).

### 3.3 Results

#### 3.3.1 The appropriate distance for photographic sampling

The appropriate distance for photographic sampling was determined to be between 10m and 20m, as no crabs visibly changed their behaviour at these distances (Fig. 3.3).



**Figure 3.3** Cumulative percentages of observations of the distance classes in which crabs responded to the observer (including standard error, based on 60 observations)

### 3.3.2 Reliability and use of data types extracted from photographic samples

The experienced observer recorded between 97.3% and 98.0% of presences of species across photo-quadrats in the first observation again in the subsequent observations and only recorded between 1.4% to 2.0% new observations (Table 3.3). Additionally subsequent observations were highly correlated to the first observation (presence/absence  $\pi$ -square correlations: 0.674 to 0.760, relative occurrence correlations: 0.949 to 0.957, absolute abundance correlations: 0.926 to 0.930). Similarly, 86.1% to 89.0% of presences recorded by the experienced observer were also recorded by each of the inexperienced observers and only 0% to 3.1% new recordings were made (Table 3.2). Correlations for relative occurrence varied between 0.936 and 0.973 and  $\pi$ -square correlations for presence/absence between 0.774 and 0.848.

**Table 3.2** Similarities in the number of individuals recorded by the experienced observer and each of the inexperienced observers

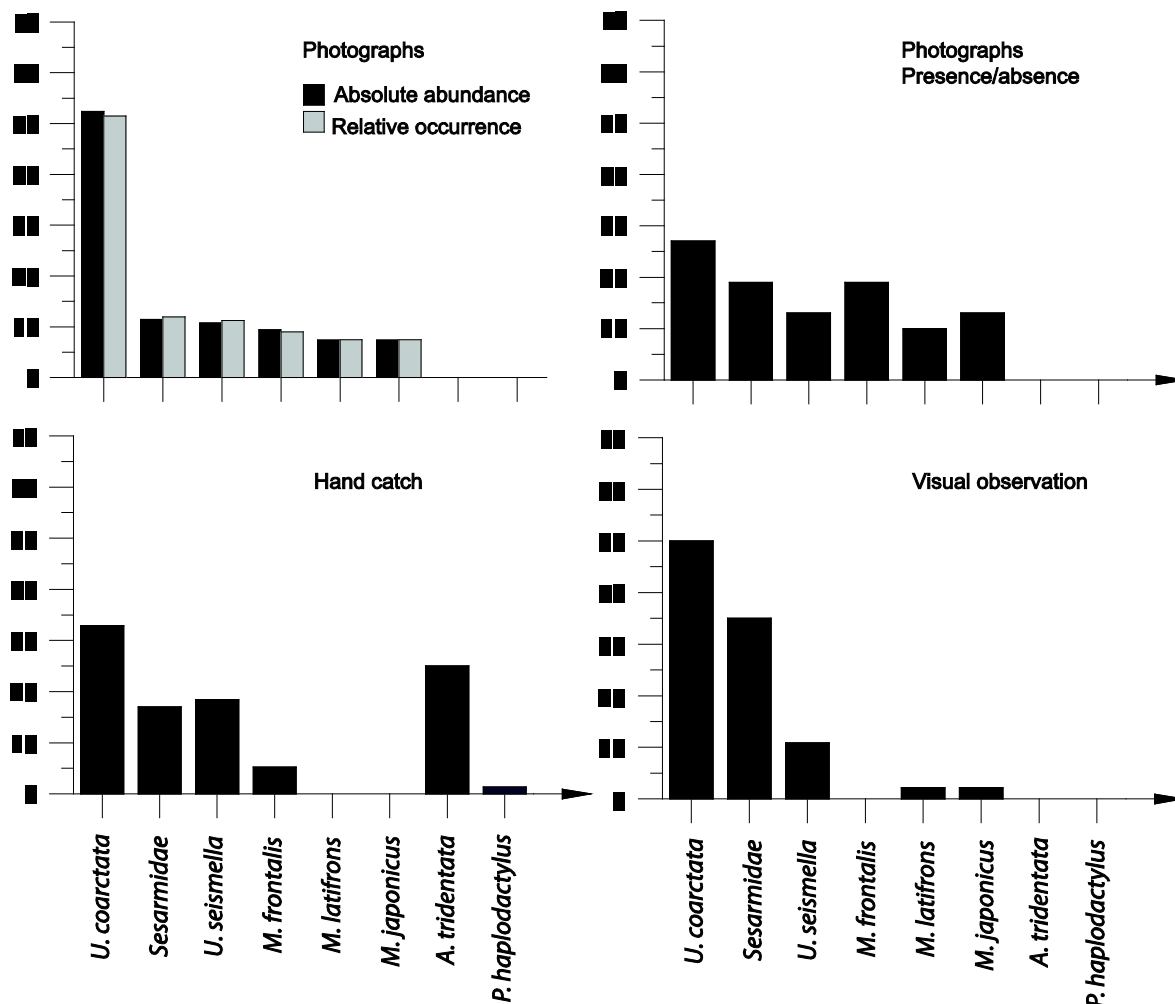
		Inexperienced observer 1		Inexperienced observer 2		Inexperienced observer 3	
		Present	Absent	Present	Absent	Present	Absent
Experienced observer	Present	31	5	31	5	32	4
	Absent	1		0		0	

**Table 3.3** Similarities in the number of individuals observed during the first observation and each of the subsequent observations by the experienced observer

		2nd observation		3rd observation		4th observation	
		Present	Absent	Present	Absent	Present	Absent
1st observation	Present	145	3	144	4	145	3
	Absent	2		3		3	



Absolute abundance and relative occurrence photography samples were dominated by the contribution of the most prevalent species: *U. coarctata*. By contrast, presence/absence photography reflected overall community composition more as contributions of different species to the sample were more equalised (Fig. 3.4).



**Figure 3.4** Relative contributions (%) of species to the total sample for absolute abundance, relative abundance and presence/absence photography, hand catch and visual observations

### **3.3.3 Comparison of photography with three traditional methods**

Overall, pitfall traps captured only 11 crabs (7 *Perisesarma longicristatum*, 3 *Australoplax tridentata* and 1 *Metopograpsus latifrons*). Absolute abundance photography sampled 155 crabs, relative occurrence photography recorded 147 occurrences, presence/absence photography recorded 54 presences, visual observation sampled 46 crabs and hand catch sampled 76 crabs (Fig. 3.4). The large species, *Metopograpsus frontalis*, *M. latifrons* and *Macrophthalmus* sp. (later identified as *M. japonicus* using targeted hand catch), contributed more to the absolute abundance photographic sample (9%, 8% and 7% respectively) than to visual observation and hand catch (0%, 2%, 2% and 5%, 0%, 0%). *U. coarctata*, a large and colourful species, dominated the visual observation (50%) and absolute abundance photographs (54%), while its contribution was reduced in the hand catch sample (33%). *M. japonicus* and Sesarmidae could not be identified to species level in photography or visual counts, while this was possible in hand catch. In particular hand catch identified 75 *Perisesarma longicristatum* and 1 *Perisesarma messa*. Finally, *Petrolisthes haplodactylus* and *A. tridentata* were only present in hand catch, contributing 1% and 25% respectively.

## **3.4 Discussion**

This study successfully developed a new photographic method to sample spatial distribution patterns of crabs on low intertidal banks and compared this new method to three traditionally used methods: hand catch, visual observation and pitfall trapping.

The traditional methods are all directly influenced by the behaviour of crabs during sampling. For example, some organisms avoid or escape from pitfall traps, while others are eaten while in the trap (Topping and Sunderland, 1992). These behaviours could explain the limited number of crabs and the taxonomic bias towards Sesarmidae observed in pitfall catches in this and other studies (Frusher et al., 1994, Salgado Kent and McGuinness, 2006). Similarly, the species composition of visual observation samples can be biased due to species specific responses to the quadrat used to outline sites for this sampling (Nobbs and McGuinness, 1999). Additionally, the presence of the researcher in both hand catch and visual observation usually results in the crabs hiding (Nobbs and

McGuinness, 1999). Hence, inter-specific differences in hiding and re-emergence behaviour, as were demonstrated for *Uca pugnax* and *Uca pugilator* (Behum et al., 2005), can bias samples obtained with these methods. To reduce this bias in visual observations, researchers usually wait a certain period after arriving at a sampling site before commencing visual observation sampling (Nobbs and McGuinness, 1999). For Sesamidae, 15 to 20 minutes was considered adequate (Salgado Kent and McGuinness, 2006), for Ocypodidae 10 minutes (Nobbs and McGuinness, 1999). Differences in hiding and re-emergence behaviour of *M. frontalis*, *M. latifrons* and *M. japonicus* could have caused their underrepresentation in visual observation and hand catch relative to the other species sampled. In conclusion, the main difference of the new photographic approach compared to the three traditional methods is that the sampling procedure does not influence the behaviour of the crabs, when conducted at the appropriate distance.

The fact that photographic sampling does not cause crabs to hide has the added advantage that sampling can be done instantly. Furthermore, the photographic procedure itself is rapid. Hence, photographic samples can be collected quickly which provides the opportunity for high resolution, large scale sampling of spatial distribution patterns of crabs. By contrast, the low numbers of crabs collected with pitfall traps are, in part, a reflection of the confined sampling range of pitfall traps for species with restricted home ranges, such as many intertidal crabs (Cannicci et al., 1996a, Layne et al., 2003, Guest et al., 2006). Similarly, hand catch, with an average 5 to 10m<sup>2</sup> sampled in each 5minute sample and visual observations with 1m<sup>2</sup> sampled in a total of 17minutes are spatially restricted over comparable time frames relative to the 10 to 20m<sup>2</sup> sampled in 2minutes with 10 photographs (Table 3.4). The spatially restricted sample size of hand catch and visual observation could provide an alternative explanation for the underrepresentation of *M. latifrons*, *M. frontalis* and *M. japonicus* in samples collected with these methods relative to photography. In fact, none of these species were the dominant species collected by any of the methods (Fig. 3.4). This indicates that these species occurred in relatively low densities for which the larger sampling area of photography provides increased detection power.

**Table 3.4** Comparison of data collection and analysis strengths and weaknesses of photography, hand catch, visual observation and pitfall trapping. (\*The experienced observer took 15 minutes and each of the inexperienced observers took 1hour to analyse the whole subset of 20 photo quadrats for relative occurrence)

	Photography	Hand catch	Visual observation	Pitfall Trapping
<b>No. of species sampled</b>	6	6	5	2
<b>Sample area (m<sup>2</sup>)</b>	10-20 (10pics)	5-10	1	Depends on mobility of species
<b>Collection time</b>	10sec./photo	5 min.	15 min.	2x10min.
<b>Analysis time*</b>	Abundance: 8min/10photos Occurrence: 7min/10photos Presence/absence: 5 min/10 photos	2min	included in collection time	2min

Just as all other sampling methods, the photographic method has certain restrictions, in particular: 1) a limited taxonomic resolution, 2) a need for background information on activity patterns and 3) an inability to provide absolute abundance data. For example, photography was unable to reliably sample small cryptic crabs and consequently underrepresented Sesarmidae and *A. tridentata*, relative to respectively visual observation and hand catch (Fig. 3.4). Additionally, it was impossible to identify *Macrophthalmus* sp. and Sesarmidae to species level. The photographic method thus has a reduced usefulness in situations where detailed taxonomic identification is required. A potential solution is to support photographic samples with hand catch to determine the range of species within the sample area. For example, by conducting additional hand catch throughout Ross River it was possible to determine that *Macrophthalmus* sp. in photographic samples was more specifically *Macrophthalmus japonicus*. Hence, when this method is applied to a new area, some pilot work, using a combination of methods, can assist in establishing the range of species available.

The instant nature of samples collected with hand catch, visual observation and the new photographic technique means that the timing of photographic sampling will determine which part of the crab fauna is examined. For instance, *Sesarmops intermedius*, *Neosarmatium meinerti*, *Cardisoma carnifex* and *Metopograpsus messor*, have bimodal activity patterns with peaks around dawn and dusk (Kyomo, 1986, Micheli et al., 1991, Eshky et al., 1995). By contrast, *Uca inversa* has a unimodal activity pattern, peaking during the middle of the day (Eshky et al., 1995). Consequently, comparative sampling needs to be done under similar environmental conditions, needs to be timed with specific target species in mind, and needs to be interpreted in light of known behavioural biases. The surface activity patterns of intertidal crabs inhabiting the low intertidal zone will therefore be subject of the next chapter.

A final limitation of photography, which also results from its instant nature, is its inability to provide absolute abundance estimates. For example, if a crab is orientated in a way that prevents identification or if a crab is obscured during sampling, identification and thus counting of that crab is impossible. Variation in biogenic structures such as roots and logs across spatially complex landscapes can cause variable shielding which might interfere with estimates of abundance and faunal composition among habitats. At a large scale the use of a high number of replicates counterbalances the shielding effects. In fact, the more replicates, the lesser the impact of missing out on an individual. Hence, presence-absence and even relative occurrence data can be collected with limited shielding effects. However, for absolute abundance data, shielding effects are a limitation of the photographic technique whose strength needs to be checked by complimentary ground truthing using selected samples collected with a different method. Absolute abundance estimates, however are also influenced by small errors in the area sampled with photography (Table 3.5). The latter sampling errors can be reduced, but usually at a cost of decreased speed and thus the ability to collect a high number of replicates over a large area. In conclusion, although reliable repeated counts of absolute abundance could be extracted from a set of photo quadrats in this study, the information that this number represents is likely to be unreliable and subject to error at a fine scale.

At the broad scale of spatial distribution patterns within an estuary, the problem of unreliable absolute abundances is unlikely to be a serious hindrance in most situations. In fact, other methods suffer biases that are at least as problematic. It is not possible to get estimates of absolute abundances of intertidal crabs using any method without intensive repeated sampling (Lee, 1998). For instance, using excavation there is the possibility that individuals escape (Salgado Kent and McGuinness, 2006). Using burrow counts there is an uncertain relationship between the number of burrows and the number of crabs (Macia et al., 2001). Using methods that rely on surface activity patterns of crabs, such as pitfalls, hand catch, visual observation and the new photographic technique, absolute abundance estimates are subject to uncertainty about the percentage of crabs that are underground at any time. Furthermore, errors in abundance estimates for a certain area result from natural variations in surface activity patterns of intertidal crabs at short time intervals (Eshky et al., 1995) and fine scale patchiness of intertidal crabs (Lee, 1998). Because of these natural and method specific errors, only substantial changes in absolute abundance can reliably be interpreted. If such changes are indeed substantial, they are likely to be captured equally adequate using relative occurrence or presence/absence data, thereby avoiding the uncertainty surrounding absolute abundances.

**Table 3.5** Error sources in photographic sampling

Error source at data collection	Solution
<p><b>The distance between observer and crabs can vary slightly, because of small errors in navigation or because banks are not always straight.</b></p>	<p>Various distance measurers can be used to reduce navigation errors. This would not reduce the speed of photographic sampling much as the boat is driven at slow speeds. Small variations in the straightness of the bank are difficult to avoid. However, they are unlikely to cause significant problems as the error created by them is random.</p>
<p><b>Bank angles are categorised in classes of 10 degrees.</b></p>	<p>Laser measurers can be used to calculate bank angles more precisely. This, however, would come at a cost of reduced speed. Additionally, finer classification of bank angles can be difficult as banks are not always perfectly to categorize under one angle. At the large scale that this method is intended and using relative occurrence or presence/absence data this problem is unlikely to cause major difficulties as the bank angle variations within a class are random.</p>
<p><b>The height of the observer can change. This affects the size of the photograph.</b></p>	<p>Using a tripod to mount the camera results in blurry photographs due to movement of the boat. Using pillows to put a small observer higher is probably best. Alternatively, have a measuring stick next to the observer, so that they stay within a certain height range.</p>
<p><b>Some banks are more rugose and have more structure, hence they have more surface in an area.</b></p>	<p>These banks can be considered as different morphological habitats and analysed as separate habitat units.</p>

Absolute abundance, relative occurrence and presence/absence data were all reliably extracted from photographs with relative occurrence and presence/absence data fastest to collect (Table 3.4). Hence, coupled with the rapid photographic sampling technique, relative occurrence and presence/absence data offer a great potential to increase the scope of spatial distribution studies on intertidal crabs over large spatial scales. Relative occurrence and absolute abundance samples were dominated by the most prevalent species. By contrast, presence/absence data reflected species composition to a greater extent (Fig. 3.4). Hence, presence/absence data give a different perspective to absolute

abundance or relative occurrence data, and the different types of data allow analysis to be tuned to the research questions. In conclusion, within the limitations of the method and focusing on species that have distinct colour patterns; the speed, low cost and ability to give reliable results irrespective of the observers' previous knowledge of intertidal crabs provides interesting perspectives to use the photographic method to bridge the gap between scale and resolution in spatial distribution patterns of crabs within the low intertidal zone.



# Chapter 4: Temperature changes influence temporal connectivity patterns of mangrove crabs

## 4.1 Introduction

Intertidal crabs are key components of tropical estuaries and are intimately linked to many fundamental ecosystem processes via trophic interactions and ecosystem engineering (Angsupanich and Aksornkoe, 1996, Apel and Tuerkay, 1999, Chapter 1). Intertidal crabs emerge from their shelter and are active on the surface during the period that their habitats are exposed by the tide (Kyomo, 1986, Micheli et al., 1991, Eshky et al., 1995). Consequently, the role of intertidal crabs in mediating key ecosystem processes is crucially dependent on successful temporal connectivity in the form of a match in the surface activity patterns of intertidal crabs and the timing of activity of other process mediating organisms (Martin, 2007, Sheaves et al., 2010). Despite the many possibilities for temporal niche segregation created by the highly dynamic estuarine environment (Lecomte and Dodson, 2004), temporal connectivity match-mismatch patterns are often neglected in ecological models (Sheaves et al., 2010). Nonetheless, climate change and urbanization has resulted in temporal shifts, creating mismatches which have already affected many fundamental ecosystem processes such as energy flow, population dynamics and species abundance (Winder and Schindler, 2004, Araújo and Luoto, 2007, Durant et al., 2007, Martin, 2007), there is an urgent need to incorporate activity patterns of intertidal crabs in ecosystem models.

The lack of incorporation of temporal connectivity patterns in ecological models partially flows on from a neglect of surface activity patterns of intertidal crabs in sampling protocols (but see Hartnoll et al., 2002). Many methods quantify the number of crabs (in terms of abundance, density or occupancy rate) based on the surface active population. For instance, photographic sampling (Salgado Kent and McGuinness, 2006, Chapter 3) and visual observation methods (Nobbs and McGuinness, 1999) only sample crabs that are active on the sediment surface. Similarly, intertidal crabs need to be seen on the sediment surface before they can be caught by hand catch (Macintosh et al., 2002, Castiglioni and

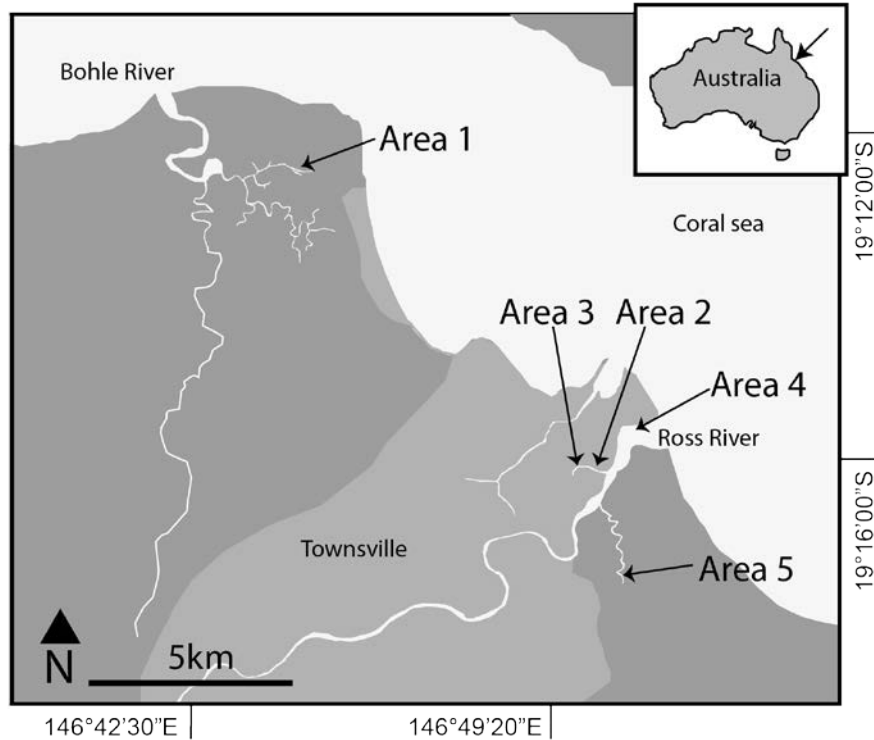
Negreiros-Fransozo, 2005) and pitfall trapping is dependent on crabs actively running into a trap (Jordão and Oliveira, 2003, Salgado Kent and McGuinness, 2006). Burrow counts and excavation are the only currently used methods that do not directly depend on surface activity patterns. However, burrow counts are often hard to interpret because the relationships between the number of crabs and the number of burrows are generally ambiguous (Lee, 1998, Jordão and Oliveira, 2003). Meanwhile, excavation is highly destructive and generally ethically unacceptable (Nobbs and McGuinness, 1999, Jordão and Oliveira, 2003). Consequently, unless highly intensive sampling is conducted, which is often financially prohibiting, surface activity patterns will influence most estimates that quantify the number of crabs. Therefore, it is important to account for this influence when developing models of estuarine processes that involve intertidal crabs.

The ability of different species to cope with changes in temperature and humidity levels throughout the day has a substantial influence on their surface activity (Knopf, 1966, Powers and Cole, 1976, Micheli et al., 1991, Wolfrath, 1993, Eshky et al., 1995). High humidity provides the necessary moisture to maintain a range of key life processes (Maitland, 1990). Consequently, it is generally assumed that the abundance of crabs peaks just after their habitat is uncovered by the tide and then gradually declines as the surface dries out (Robertson et al., 1981, Weisberg and Ranasinghe, 1997, Zeil and Hemmi, 2006). Negative correlations with increasing temperatures (Eshky et al., 1995) fit into this generally assumed concept because increasing temperatures are partially responsible for the sediment drying out over the tidal period. However, in concordance with the adaptive feeding hypothesis, increasing temperatures might also boost the productivity of algae, a main food item for many intertidal crabs, which could lead to increasing surface activity of these crabs at higher temperatures (Shaw and Tibbetts, 2004). Additionally, biological interactions can also further influence the shape of surface activity patterns (Cannicci et al., 1998). Consequently, to improve ecological models of estuarine processes that involve intertidal crabs, it is critical to incorporate activity patterns in these models and to account for their influence on estimates of crab numbers. Therefore, this chapter aims to determine the patterns and drivers of surface activity of intertidal crabs to be able to account for them when sampling and modeling intertidal crab assemblages using photographic methods in subsequent chapters in this thesis.

## 4.2 Methods

### 4.2.1 Study area

Sampling was conducted in Ross River and Bohle River estuaries, North Queensland, Australia (19°16'00"S, 146°49'20"E and 19°12'00"S, 146°42'30"E, Fig. 4.1) over eight days across the dry season of 2010 and 2011. Virtually no rainfall was recorded (average monthly rainfall: 22.6mm in June 2010, 1.8mm in July 2010 and 15.8mm in June 2011, data Bureau of Meteorology, Queensland Government) and average monthly temperatures varied between minimum 12.9°C and maximum 26.7°C (Bureau of Meteorology, Queensland Government). Semidiurnal tides prevail in both estuaries and sampling was conducted during daytime spring tides with low tide less than 1m and high tide above 2.3m. Five study areas were selected (Fig. 4.1). Each contained a high density of crabs. Area 1, 2 and 3 contained an exposed mud bank bordered by *Avicennia marina* vegetation which was inhabited by *Uca coarctata* mixed with patches of *Perisesarma longicristatum*. Additionally, area 1 and 3 also contained a saltpan occupied by *Uca signata*. Area 4 was an exposed mudflat dominated by *Macrophthalmus japonicus* and area 5 consisted of a rock wall made up of boulders and the remains of a bridge. This area was populated by *Metopograpsus latifrons* and *Metopograpsus frontalis*. Ross River runs through the city of Townsville resulting in anthropogenic debris and pollution inputs in the areas studied. Area 1, which is the only area within Bohle River, lies within a national park. However, the Bohle River receives sewage inputs from a treatment plant located upstream.



**Figure 4.1** Location of sampling areas in Bohle River and Ross River, North Queensland, Australia

#### **4.2.2 Sample collection**

Cameras were used to monitor the abundance of intertidal crabs over the tidal period. The five areas were sampled on different days and distinct randomly selected sites were chosen each time. Two cameras, five meters apart were positioned per site. These cameras were mounted on a two meter long pole placed under an angle of 20° from vertical. Cameras used were Sony DCR-SR47 HDD handycam video recorders with a resolution of 0.5megapixel. Additionally, Pentax Optio 33WR photo cameras with time lapse function and 3.2megapixel resolution were trialed on 24 and 26 July 2010. Cameras faced straight down and recorded a replicate sample of 1m<sup>2</sup> and 1.5m<sup>2</sup> for video and time lapse cameras respectively. Cameras were installed during ebb when there was two to three centimeters of water remaining on the site. Video cameras were then run continuously and time lapse cameras in 15 minute intervals until the site flooded again. Individuals of each species per replicate sample were counted by analyzing one frame every 15 minutes. The first data point was taken 15 minutes after the cameras were set up

to avoid influence of the presence of the researcher on the crabs' behavior. All crabs that could be identified were counted. Simultaneously, data on temperature and humidity at the scale of the site were collected with a TESA WS1081PC weather station which could collect data at two different locations. On 30 June 2011, the weather station failed and no data were collected.

#### **4.2.3 Statistical analysis**

Data on crab abundances were pooled per site and the pattern of abundance over the tidal period was interpreted from a distance weighted least squares smoothing function with a stiffness of 0.25. Additionally, partial correlations with temperature and humidity were calculated. To allow these correlations to be made, data of abundance, temperature and humidity were standardized to the lowest value recorded and expressed as a percentage relative to the highest value recorded for abundance, temperature and humidity per pattern studied.

### **4.3 Results**

A uni-modal pattern with a shifting peak was observed for crab abundances over the tidal period in the majority of the 16 patterns analyzed (Appendix 2). An exception was the pattern of *P. longicristatum* for which abundances remained at a steady level until the very last moment. The data were generally well represented by the smoother, with the main exceptions being, on 29 June 2010, one of the patterns of *U. coarctata* and the pattern of *U. signata*. Additionally, because *M. frontalis* was only represented by a maximum of 2 individuals at any time, a pattern for this species was not analyzed. All other patterns were based on peak abundances between 7 and 35 and between 20 and 141 crabs, using the video and time-lapse cameras respectively.

Activity patterns of intertidal crabs were generally positively correlated with temperature, while only patterns of *U. signata* and *M. japonicus* showed respectively a low positive and a negative correlation with humidity (Table 4.1). An exception to the positive correlation with temperature was the pattern of *U. coarctata* on 29 June 2011 which displayed a low negative correlation with temperature. *P. longicristatum* was not substantially correlated

with temperature or humidity. Also, on 18 July when time lapse recordings were conducted, no correlation was found with temperature or humidity for *M. japonicus*. Finally, two activity patterns of *U. coarctata* also did not show any correlations with temperature or humidity.

**Table 4.1** Partial correlation coefficients of the different activity patterns with temperature and humidity

<b>Species</b>	<b>Day</b>	<b>Temperature</b>	<b>Humidity</b>
<i>U. coarctata</i>	19/06/2010	0.57	-0.03
<i>U. coarctata</i>	21/06/2010	-0.15	-0.29
<i>U. coarctata</i>	26/07/2010	0.81	0.08
<i>U. coarctata</i>	26/07/2010	0.80	0.08
<i>U. coarctata</i>	29/06/2011	-0.38	-0.22
<i>U. coarctata</i>	29/06/2011	0.10	0.10
<i>U. signata</i>	29/06/2011	0.55	0.44
<i>M. latifrons</i>	19/07/2010	0.76	0.33
<i>P. longicristatum</i>	26/07/2010	0.12	-0.32
<i>M. japonicus</i>	24/07/2010	0.67	-0.62
<i>M. japonicus</i>	18/07/2010	0.27	0.22

## 4.4 Discussion

Shifts in the use of temporal niches by intertidal crabs over the tidal period in correlation with changes in temperature and humidity could affect the temporal connectivity between intertidal crabs and other process mediating organisms. Patterns of surface activity displayed moderate to strong positive correlations with temperature for the majority of intertidal crabs investigated in this study. This agrees with previous results on *Uca inversa* (Eshky 1995), *Metopograpsus frontalis* (Shaw and Tibbetts, 2004) and *Uca pugilator* (Knopf, 1966). By contrast, a correlation with humidity was only found for *U. signata* which occupies habitats where high temperatures are often recorded (Nobbs, 2003). Potentially, crabs occupying habitats where higher temperatures occur are more susceptible to other environmental factors such as low humidity. Additionally, the correlation with temperature

was variable both between species and within *U. coarctata*, indicating additional factors were involved. It is likely a combination of specific temperature and humidity conditions are needed for crabs to be active on the sediment surface. Persistent changes in either factor are therefore likely to influence the shape of the surface activity pattern over the tidal period of intertidal crabs and affect the nature of the biological interactions they mediate.

The interaction between temperature and the surface activity pattern of intertidal crabs is likely a result of adaptive feeding. According to the adaptive feeding hypothesis organisms are most active when their food source is most abundant/productive (Shaw and Tibbetts, 2004). For example, the surface activity of *Metopograpsus frontalis* increases during warmer periods of the day, corresponding to an increased productivity of their algal food sources (Shaw and Tibbetts, 2004). Similarly, adaptive feeding could explain the increased surface activity in relation with higher temperatures observed for *M. latifrons*, a macro-algal grazer (Dahdouh-Guebas et al., 1999, Poon et al., 2010, Nordhaus et al., 2011), and for *Uca* spp. and *Macrophthalmus* spp., sediment deposit feeders that gain a large proportion of their nutrition from benthic microalgae (Hsieh et al., 2002, Kanaya et al., 2008, Nagelkerken et al., 2008). The importance and complexity of adaptive feeding as a mechanism influencing surface activity patterns of intertidal crabs is also illustrated by a decrease in the production of feeding pellets of *Uca* spp. in a sewage impacted site compared to a non-impacted site (Bartolini et al. 2011). In the former sewage impacted site, feeding requirements of *Uca* spp. are fulfilled faster because of the increased algal productivity (Bartolini et al. 2009).

By contrast, *U. coarctata*, *U. signata* and *M. japonicus* construct burrows (Kristensen, 2008) and the rocky habitat of *M. latifrons* has ample crevices. Such shelter possibilities reduce physiological stress by providing a recharge point where temperatures are lower and water can be replenished (Eshky et al., 1995). Not all intertidal crab have this possibility. For example, *Metopograpsus messor* does not construct burrows and its dark colors are conducive to heat absorption (Eshky et al., 1995). Consequently, *M. messor* needs to avoid desiccation by sheltering in shaded areas and reducing its surface activity during periods of high temperatures (Eshky et al., 1995). For the latter type of species, physiological stress is likely to be of greater importance. Nonetheless, for many intertidal

crabs physiological stress is unlikely to be a major hindrance in the surface activity of many intertidal crabs.

The observed shifting uni-modal peak in abundance of surface active crabs has implications for the timing of when sampling should be conducted, because it could confound with estimates of abundance obtained with most current methods, including the photographic method developed in Chapter 3 (Nobbs and McGuinness, 1999, Salgado Kent and McGuinness, 2006, Jordão and Oliveira, 2003). For instance, when ecological models are based on abundance estimates obtained from a single point in time, or when different sites are compared based on consecutive samples collected over the tidal period, results could be misleading. Hence, patterns in surface activity should be considered when designing studies. This could be achieved by restricting sampling to a narrow time window, by taking repeated samples over the tidal period, by recording temperature during sampling or by down weighing the influence of variations in activity patterns by recording occurrence rather than abundance.

Although cameras are a very useful method that could substantially increase knowledge of surface activity patterns of intertidal crabs, the segment of the crab population studied could be influenced by the resolution capacities of different camera types used. Previous examinations of surface activity patterns of intertidal crabs were generally limited in temporal replication, with samples over the tidal period taken at 30 minute (Kyomo, 1986) to hourly intervals (Micheli et al., 1991, Eshky et al., 1995, Shaw and Tibbetts, 2004). By contrast, video cameras have the possibility to continuously monitor the activity over the tidal period and time lapse cameras can take photographs every minute. The time-lapse cameras had a higher resolution which allowed a larger area and also smaller and more cryptic individuals to be observed. This higher resolution is beneficial for studying *Uca* spp., where females lack a large colorful claw which makes them less conspicuous than males. Indeed, the maximum number of individuals sampled with video cameras consisted mainly of males, while the individual peaks observed with time-lapse cameras gave a more even distribution of males and females. However, males usually spend more time on the surface than females, performing defensive and mate-attracting behavior or feeding for longer periods to compensate for their larger size and for only having one functional feeding claw (Emmerson, 1994). The higher resolution and thus a more complete



representation of the whole population could be one of the reasons why no correlation was found between the surface activity pattern of *M. japonicus* and temperature or humidity when using time-lapse recordings, while such correlations were established based on video-camera observations. In conclusion, the segment of the population studied, in terms of sex or ontogenetic stage should be considered when examining surface activity patterns of intertidal crabs using camera methods.

# Chapter 5: A conceptual model of habitat associations of intertidal crabs in a dry tropical estuary

## 5.1 Introduction

Intertidal crabs are abundant components of tropical estuaries (Hartnoll et al., 2002, Skov et al., 2002, Jaroensutasinee and Jaroensutasinee, 2004). They are basal consumers linking detritus and primary producers to higher trophic levels, such as birds and fish (Sheaves and Molony, 2000, Bouillon et al., 2002). Additionally, they are ecosystem engineers (Kristensen, 2008), affecting sediment composition (Botto and Iribarne, 2000, Escarpa et al., 2004), productivity (Koch and Wolff, 2002, Werry and Lee, 2005), vegetation structure (Bosire et al., 2005), faunal composition (Dye and Lasiak, 1986, Botto et al., 2000) and energy fluxes (Wolff et al., 2000). Thus intertidal crabs are intimately linked to many fundamental ecological processes. Particularly within the low intertidal zone their influence can be far reaching because regular tidal inundation of this zone enables ecological connections to be made between the resident crab fauna and transient estuarine components (Cannicci et al., 1996a, Botto et al., 2000, Sheaves and Molony, 2000, Chapter 1). However, the exact patterns of ecological connectivity, and thus the contributions of crab species to estuarine ecosystem processes, vary depending on the spatial distribution patterns of those crabs across the low intertidal landscape.

Most studies on spatial distribution patterns of intertidal crabs focus on small, within-site or within-transect scales (Koch et al., 2005, Arruda Bezerra et al., 2006, Takeda, 2010, Chapter 1). This is a reflection of methodological constraints which prevent replicate sampling over a large area within a short time frame (Chapter 3). However, the applicability of results obtained from such small scale studies at larger landscape scales is restricted, because of a lack of understanding of the mechanisms structuring assemblages at these larger scales. For instance, existing work has established relationships between the spatial distribution of intertidal crabs and specific environmental factors, such as sediment organic matter content, sediment grain size, salinity, dominant vegetation types and tidal height (Weis and Weis, 2004, Koch et al., 2005, Arruda Bezerra et al., 2006,

Ravichandran et al., 2007, Takeda, 2010). However, the relative importance of these environmental factors in determining spatial distribution patterns of intertidal crabs at landscape scales has not been established.

The full environmental potential of the low intertidal landscape is also not addressed by small scale studies. In fact, they can only give snapshots of information regarding spatial distribution patterns in the part of the low intertidal landscape that was studied. Additionally, most studies have been conducted on a single bank type within the low intertidal zone; generally low angle mud banks with little structural complexity (Lee, 2008, Vergamini and Mantelatto, 2008, Takeda, 2010). Hence, despite the high structural diversity of the low intertidal zone, with some areas devoid of structure and others containing complex three-dimensional structures (Lee, 2008), the habitat heterogeneity of the low intertidal zone and the pattern of intertidal crab assemblages relative to this heterogeneity are underrepresented. Similarly, the few studies that have looked at larger, cross-estuary patterns usually only sampled specific sites along the estuary and thus have also neglected the full environmental potential of the low intertidal zone (Snelling, 1958, Ness, 1972). In conclusion, a conceptual model of the spatial distribution patterns applicable within the low intertidal landscape of tropical estuaries is lacking. Such spatial knowledge is critical to allow the integration of the value of the functional roles of intertidal crabs in landscape scale ecosystem models (Wolff et al., 2000).

Predictive habitat modeling can be used to conceptualize and test habitat associations of organisms at large scales. Consequently, it can determine the pattern of spatial distribution of organisms at landscape scales relative to spatial niches determined by environmental parameters. Habitat modeling relies on the development and testing of a hypothesis about the spatial association between species and a combination of environmental variables (Guisan and Zimmermann, 2000). A conceptual model of habitat associations of the species investigated can be interpolated in the context of the model (Guisan and Zimmermann, 2000), based on a limited number of surveys. This is cost and logistically efficient compared to extensive and often financially prohibitive long term monitoring projects, especially considering the often labor intensive methods used to sample spatial distribution patterns of intertidal crabs (Wintle et al., 2005, Chapter 3). Predictive habitat modeling has been used extensively in ecological surveys of spatial

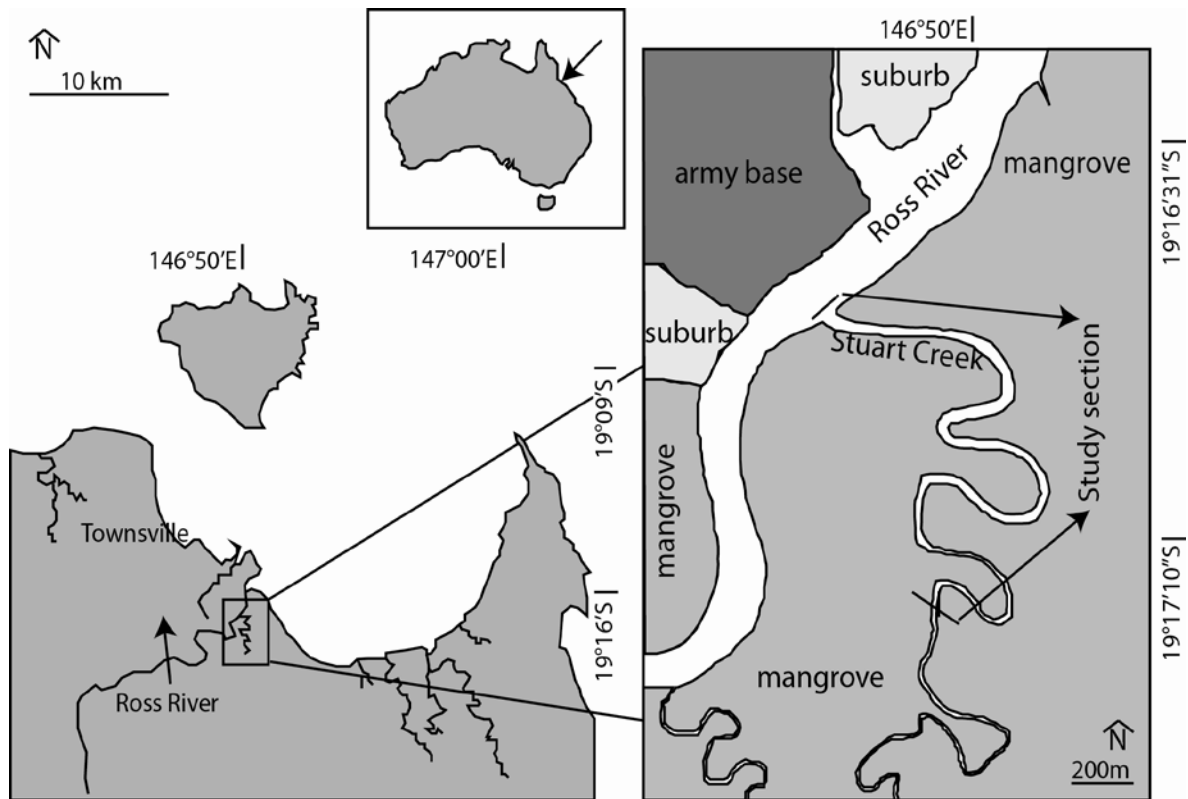
distributions (vegetation: Guisan and Zimmermann, 2000, birds: Fielding and Bell, 1997, mammals: Wintle et al., 2005) as well as in management and conservation planning (Guisan and Zimmermann, 2000, Wintle et al., 2005).

This chapter aims to improve understanding of the spatial distribution patterns of intertidal crabs within the low intertidal zone of tropical estuaries. Therefore, a simple conceptual model is constructed representing the main trends in habitat association of different species of crabs at an estuary-wide scale. This conceptual model is constructed using photographic sampling, to take advantage of its ability for rapid representative data collection over extensive spatial scales, coupled with predictive habitat association modeling, which allows for the development and testing of habitat association models of individual species.

## 5.2 Methods

### 5.2.1 Study location

Sampling was conducted in a section of Stuart Creek, North Queensland, Australia, (19°17'S, 146°50'E, Fig. 5.1), from its downstream junction with Ross River estuary to a point 3km upstream where sampling by boat was restricted by the water depth at low tide. In this section, the low intertidal zone of Stuart Creek contains a diversity of bank types. Bank angles range from horizontal to vertical. Vegetation lining these banks can be classified in four groups: 1) mangrove vegetation growing between mean sea level and mean high water at neap tide including *Rhizophora stylosa*, *Avicennia marina* and *Aegiceras corniculatum*; 2) Mangrove vegetation above mean high water at neap tide, predominantly *Ceriosps* spp. and *Burquiera gymnorhiza*; 3) grasses occurring above mean high water at neap tide, chiefly *Sporobolus virginicus* and 4) bare banks. Different structural elements are present, including logs, clumps of *S. virginicus*, pneumatophores, prop roots, cable roots and buttress roots. Very fine sand to silt aggregates dominate the sediment grain size classes of the Udden Wentworth scale (Wentworth, 1922).

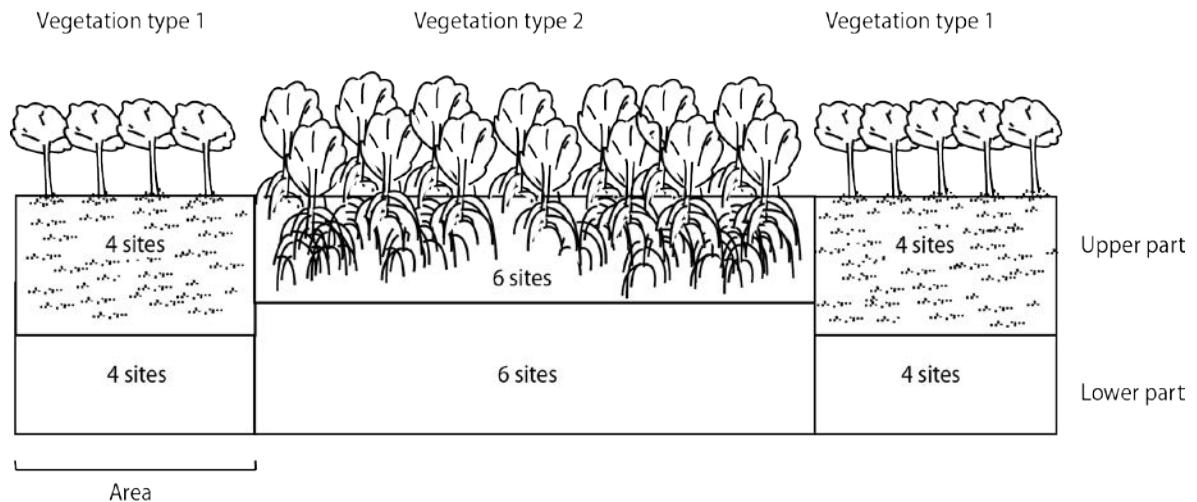


**Figure 5.1** Location of Stuart creek with indication of study section

Stuart Creek is part of a dry tropical estuary, characterized by strong seasonal variations in rainfall. Usually, 78.5% of the average annual rainfall occurs during a short period in summer, between December and March, when temperatures are around 31°C (Bureau of meteorology, data for Townsville between 1940 and 2011). The remainder of the year is dry with lowest average temperatures of around 26°C (Bureau of meteorology, data for Townsville between 1940 and 2011). The study section of Stuart Creek is under daily influence from semidiurnal tides with tidal ranges greater than 3m on spring tides. Lowest spring tides occur during the day in the dry season and at night in the wet season. Sampling trips were conducted once per year in the pre dry (April to May), dry (July), pre wet (September to October) and wet (December, January) season between April 2009 and July 2011. Wet season samples were collected just before the main rainfall events because the low intertidal zone often remained flooded during these events, prohibiting sampling. Total annual rainfall in 2009 and 2010 was high (1989.4mm and 2006.4mm respectively, Bureau of meteorology), reducing salinities in the study section during wet and post-wet seasons relative to local sea water levels of about 35 ‰.

### 5.2.2 Sample collection

A stratified random sampling strategy was employed where the whole low intertidal zone within the study section was divided in areas, based on changes in dominant vegetation (Fig. 5.2). Each area was then divided in an upper and lower part, based on changes in structural complexity and/or sediment type (mud, sand or rock). A maximum of six sites, 15 to 20m long and 10m apart, were then randomly selected within each part of each area, depending on its size. This sampling strategy was chosen to maximize representation of the environmental heterogeneity along and across the low intertidal zone. Vegetation was chosen to identify areas because it has previously been associated with intertidal crab distribution (Dahdouh-Guebas et al., 2002) and because it allows for a clear division in areas with different structural heterogeneity. The 10m gap between sites ensured that sites were spatially independent of each other, because adult intertidal crabs have home ranges restricted to a few square meters (Cannicci 1996a, 1999, Zeil and Henmi 2006).



**Figure 5.2** Example of the stratified sampling design used, with indication of upper and lower parts within areas as a basis for site selection

The total number of sites ranged from 108 to 118 per trip, except during April 2009 when only the first 2 km of Stuart Creek, with 54 sites was surveyed. Sampling was conducted in one day for each side of Stuart Creek, with no more than 3 days between left and right side sampling. All sampling was done in a short 3 hour window during ebb spring tides

starting when the upper parts of the low intertidal zone became exposed. This was to reduce variations in crab numbers recorded between sites due to changes in the surface activity pattern of intertidal crabs (Chapter 4). Spring tides were selected because a maximum area of the low intertidal zone is exposed at those times. All sampling was conducted on days with low tide between 12am and 3pm to reduce the potential effects of temperature and humidity differences at various times of day on observations of crabs (Chapter 4).

Relative occurrences of crabs in each site were sampled with photography following the protocol described in Chapter 3. Relative occurrence was chosen as appropriate data for the scale of this study, rather than relative abundance. Relative occurrence is less sensitive to small scale variations in surface activity patterns (Eshky et al., 1995, Chapter 4) and patchiness of crabs (Lee, 1998), and allows for faster processing of data. Relative occurrences within standardized photo quadrats were averaged at the site level. Identification of species on photographic samples was compared to voucher specimens collected using a variety of sampling techniques (hand catch, pitfall trapping and visual observation) throughout the study area.

The structure of each site was described in terms of canopy overhang (in 10% classes), bank angle (in 10° classes) and one of the four vegetation categories. Additionally, the percentage of a site (measured in each photo quadrat in 10% classes and averaged over the site) covered by logs, pneumatophores, grass, prop roots, other roots (cable and buttress roots) and structure (sum of logs, prop roots and other roots) was recorded. The environmental variables chosen are easy to measure in the field and can therefore be used to outline simple, defined habitats relevant to the aims of this study.

### **5.2.3 Statistical analysis**

Sites were grouped for each individual species using predictive habitat modeling (Guisan and Zimmermann, 2000). First, a model of within-estuary occurrence was made using presence/absence data at the site level as a categorical dependent variable. This step enabled sites where a species occurred (termed occupied sites) to be separated from sites where it did not occur. Subsequently, occupied sites were further analyzed to

determine clusters of sites with similar relative occurrences. Both models were constructed using data from July 2010, September 2010, December 2010 and April 2011 as the training set and the other six trips as individual tests. July 2010 was randomly chosen by dice-throw, and the other training trips subsequently chosen because together they formed a sequence of one year of data following July 2010. In both models, vegetation class and season were the categorical predictors and bank angle, canopy overhang and average percentage of logs, grass, pneumatophores, prop roots, other roots and structure covering the substratum at the site level were the continuous variables.

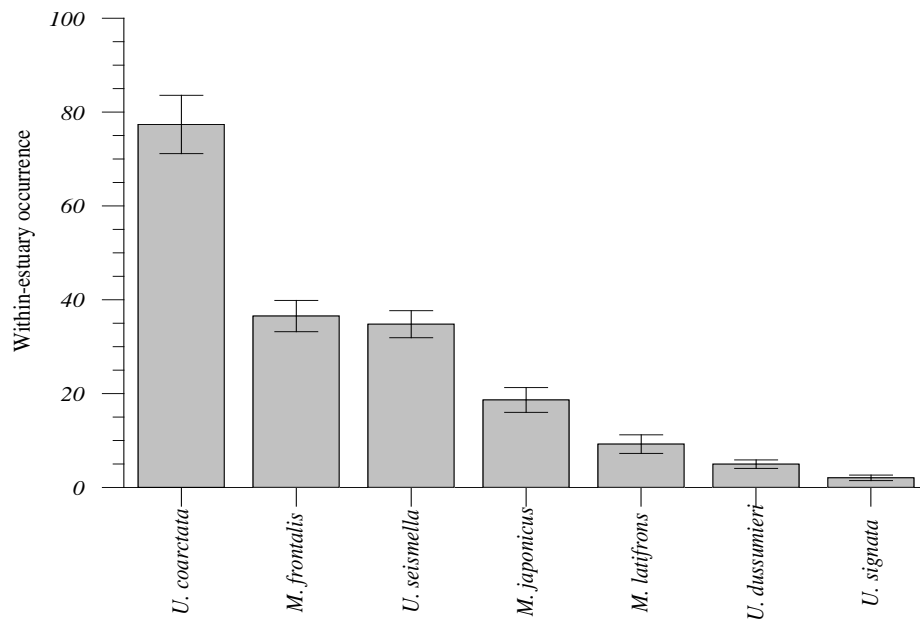
A simple model explaining the main trends in the data was developed using classification and regression tree analysis (CART: De'ath, 2002), a technique commonly employed in predictive habitat modeling (Guisan and Zimmermann, 2000). CARTs were resolved using the GINI index for presence/absence data, and least squares deviation for relative occurrence data. Resulting CARTs were then pruned via test sample cross validation, using the test trip misclassification (1=total misclassification, 0= perfect classification) as cross validation cost (CV cost). Across the 6 tests, the smallest tree with a CV cost within 1 standard error of the minimum CV cost was selected. The misclassification error of this final model with the original training data was calculated, via 10 fold cross validation.

The predictive ability of within-estuary models was assessed via sensitivity analysis, calculating both sensitivity and percentage of false positives. Sensitivity quantifies the number of sites observed with the species present that are predicted to have the species present. The percentage of false positives is the percentage of sites predicted with a species present where the species is observed to be absent. Models with high sensitivity and low false positive rate were preferred as they allow precise classification of sites with a high probability of finding the organism present. Predictive ability of within-site models was assessed by analyzing misclassification errors and by comparing the relative contribution of the average relative occurrence of a species in each of the predicted clusters across the test trips.



## 5.3 Results

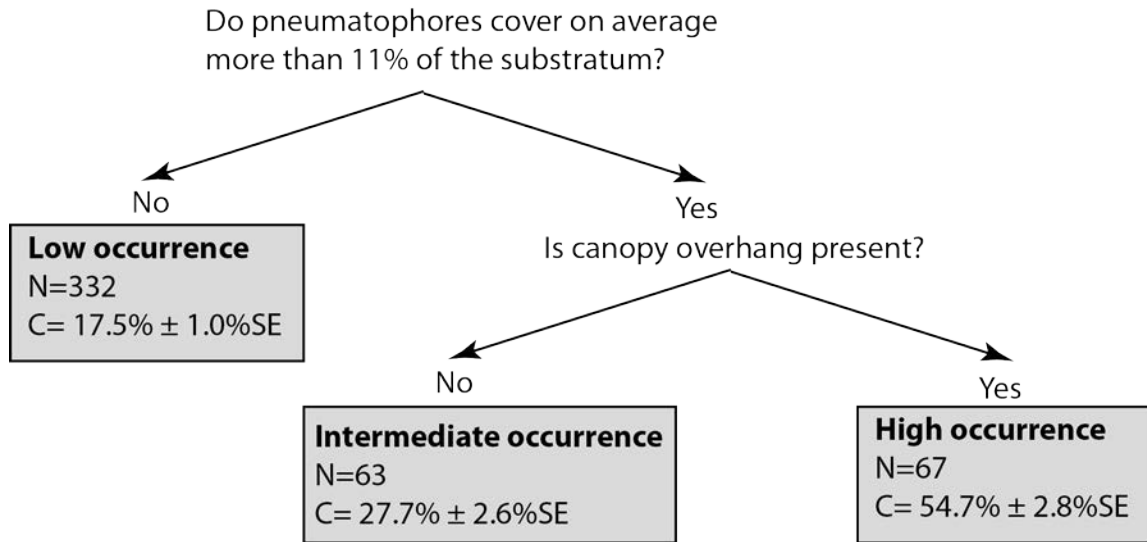
*Uca coarctata* (Ocypodidae) was the dominant species across the study, with high presence across sites (Fig. 5.3). The presence of both *Uca seismella* (Ocypodidae) and *Metopograpsus frontalis* (Grapsidae) across sites was around half that of *U. coarctata*. *Macrophthalmus japonicus* (Macrophthalmidae), *Uca dussumieri* (Ocypodidae), *Uca signata* (Ocypodidae) and *Metopograpsus latifrons* (Grapsidae) were present at low levels.



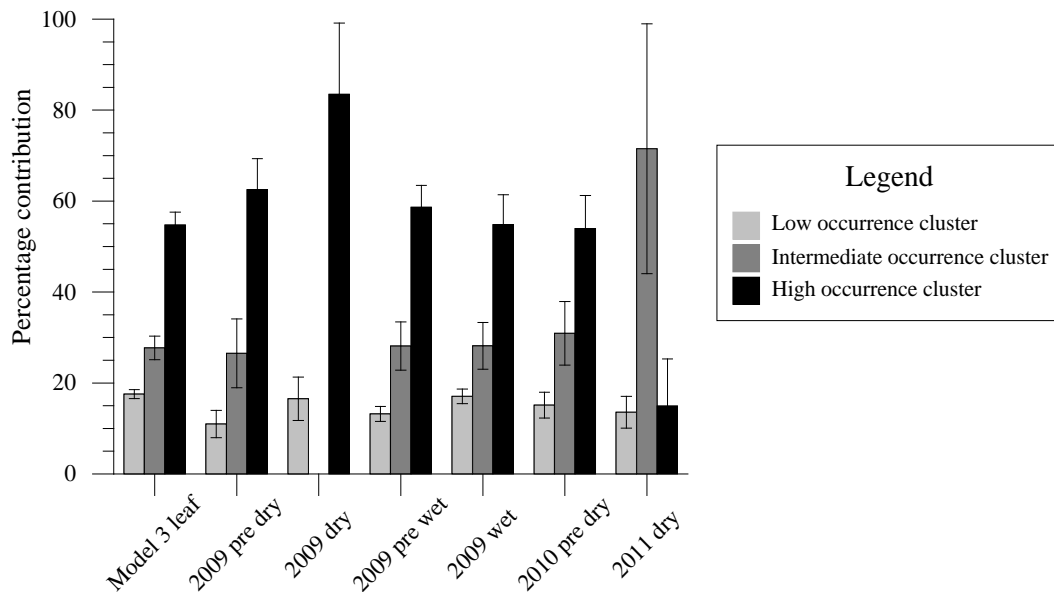
**Figure 5.3** Mean percentage within-estuary occurrence ( $\pm$ SE) of species across the study period

### 5.3.1 *U. coarctata*

CART analysis could not separate sites based on presence/absence data, possibly because *U. coarctata* occurred in nearly all sites. However, using relative abundance data, sites were clustered in three groups (Appendix 3.1, Fig. 5.4). Misclassification errors for the three leaf model were low in each of the six test trips (mean:  $0.0156 \pm 0.0019$ SE, range: 0.0087 and 0.0214) and the contribution of the relative occurrence of *U. coarctata* relative to the total relative occurrence across the different predicted clusters was comparable in all test trips except the 2009 and 2011 dry season trips (Fig. 5.5).



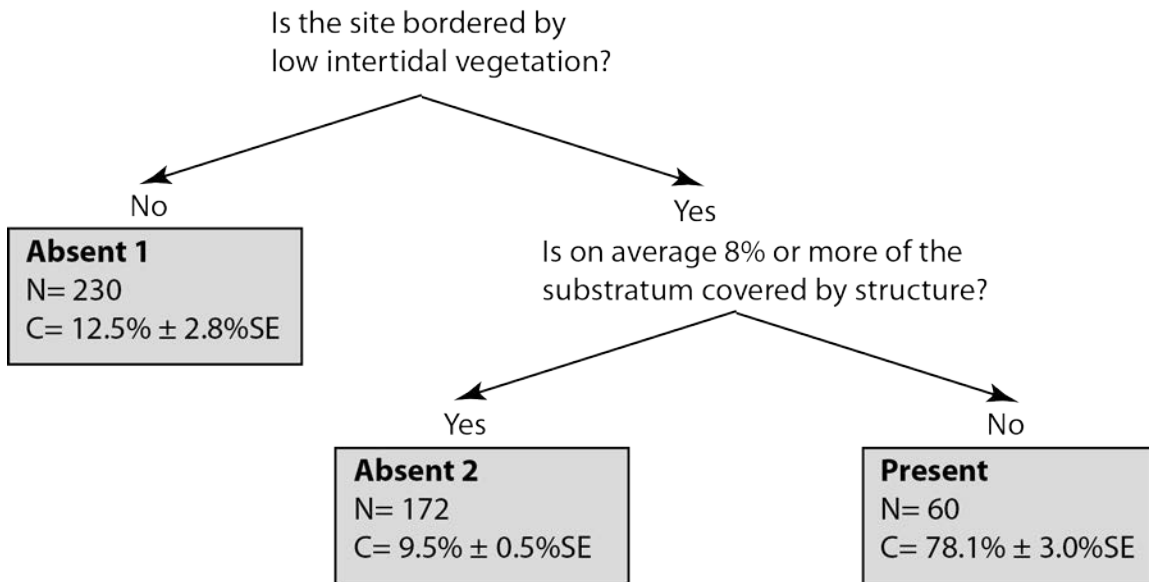
**Figure 5.4** CART model for within-site occurrence of *U. coarctata*, including the number of sites (N) and mean contribution (C) of within-site occurrences per cluster relative to the sum of the within-site occurrence across all clusters, as observed in the training data



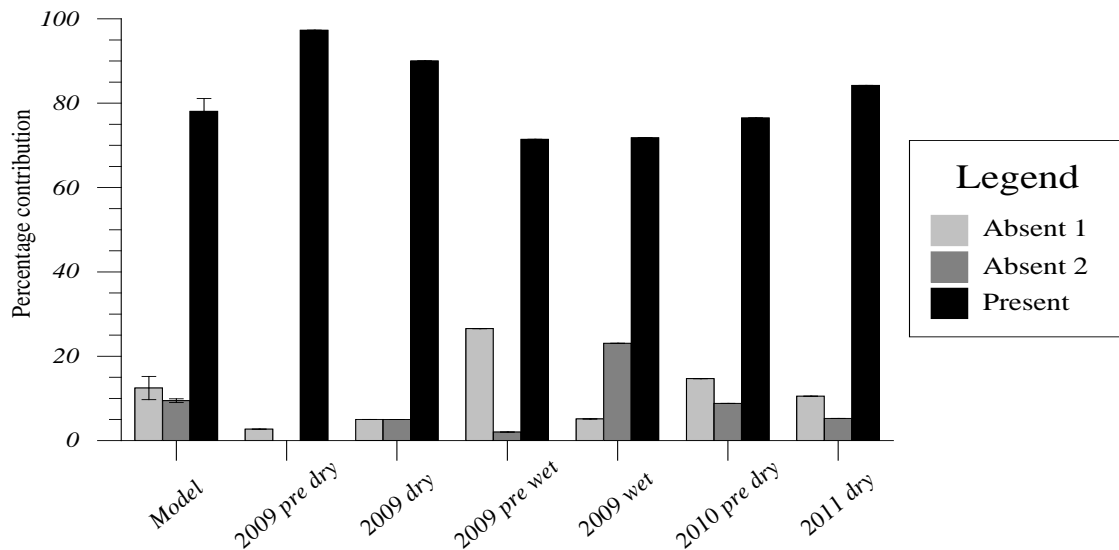
**Figure 5.5** Percentage contribution of the relative occurrence of *U. coarctata* in each cluster relative to the total relative occurrence across clusters per trip ( $\pm$ SE) in the model and test trips

### 5.3.2 *U. seismella*

CART modeling identified three groups of sites based on presence/absence data (Fig. 5.6). Occupied sites were bordered by low intertidal vegetation and contained little structural complexity. Predictions of this model were good (Fig. 5.7), with high sensitivity (mean:  $81.9\% \pm 4.3\%SE$ , range: 71.4% to 97.3%) and low percentages of false positives (mean:  $21.7\% \pm 3.1\%SE$ , range: 14.7% to 31.3%) for observations in occupied sites versus observations in all other sites. Further CART analysis of differences between occupied sites based on relative occurrence data did not produce valid models.



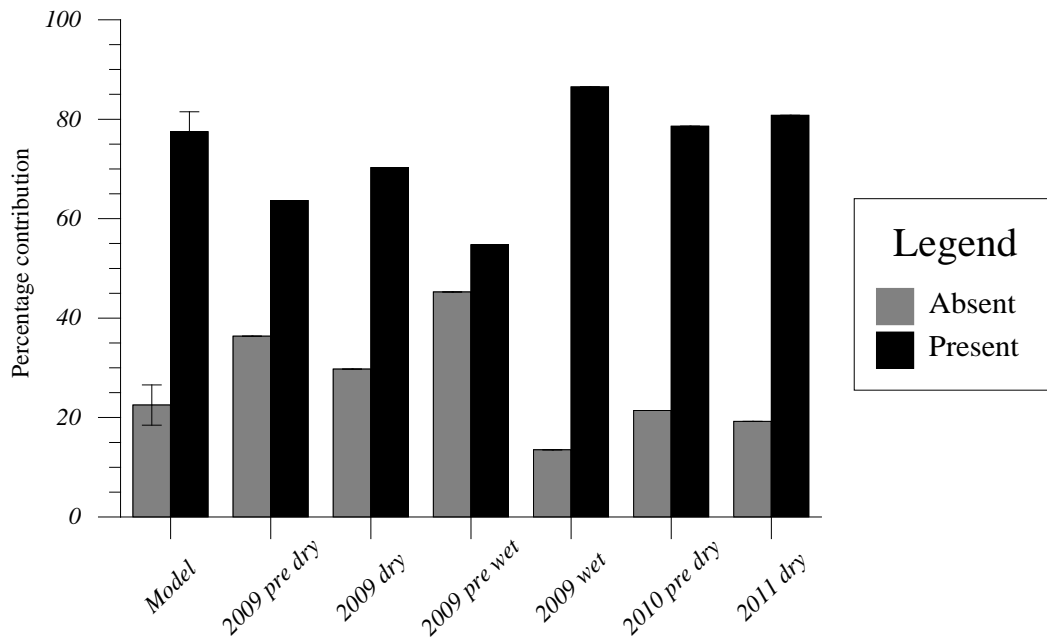
**Figure 5.6** CART model of presence/absence of *U. seismella* with indication of the number of sites (N) and the contribution (C) of *U. seismella* presences in each group relative to the total number of presences recorded across all groups, as observed in the training data



**Figure 5.7** Percentage contribution of the presence of *U. seismella* in each group relative to the total number of presences across all groups per trip ( $\pm$ SE) for the training data and test trips

### 5.3.3 *M. frontalis*

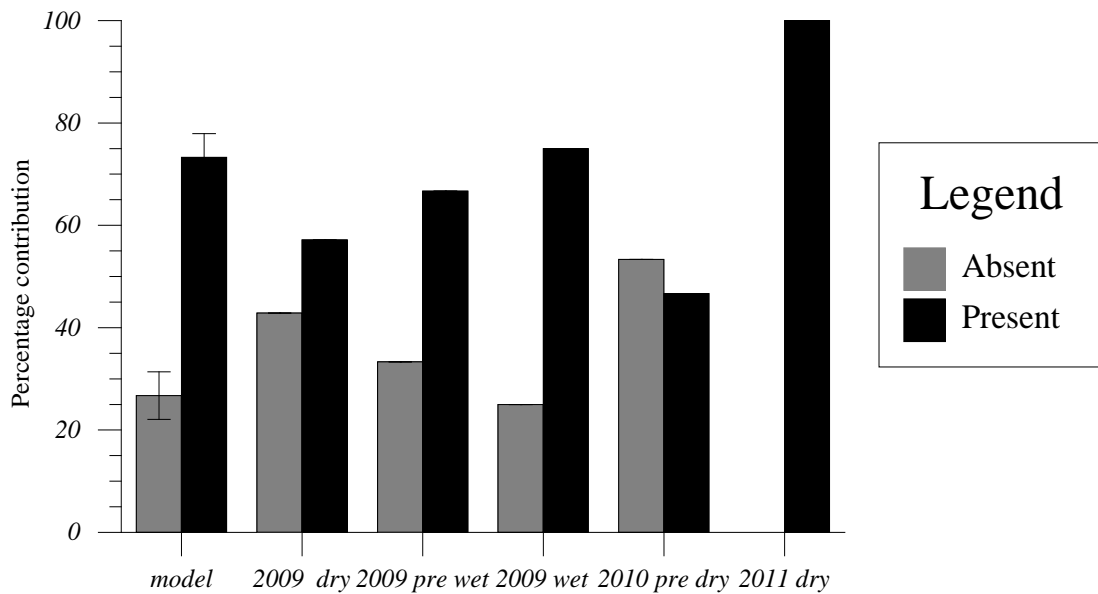
A two leaf CART model using presence/absence data of *M. frontalis* (Appendix 3.2) predicted occurrence in sites with structure covering at least 4% of the substratum. Observations within the 2009 wet, 2010 pre dry and 2011 dry test trips fitted the predictions better than the 2009 pre dry, dry and pre wet test trips (Fig. 5.8). Nonetheless, sensitivity for observations within occupied sites versus observations in all other sites were high across all trips (mean: 72.4%  $\pm$  4.8%SE, range: 54.8% to 86.5%), and the percentages of false positives, although variable, were acceptable (mean: 27.2%  $\pm$  5.8%SE, range: 13.6% to 49.4%). A CART of differences between occupied sites based on relative occurrences was developed, but testing of this model did not deliver predictable patterns (Appendix 3.2).



**Figure 5.8** Percentage contribution of the presence of *M. frontalis* in each group relative to the total number of presences across all groups per trip ( $\pm$ SE) for the training data and test trips

### 5.3.4 *M. latifrons*

No *M. latifrons* were recorded during the 2009 pre dry season and only few *M. latifrons* were sampled within the training and other five test trips (mean:  $10.7 \pm 2.3$ SE). Nonetheless, a two leaf CART model predicted *M. latifrons* to be present in sites where at least 22% of the substratum was covered by structure (Appendix 3.3). Predictions of this model across the test trips were variable, but generally satisfactory (Fig. 5.9), with acceptable sensitivity (mean:  $69.1\% \pm 9.1\%$ SE, range: 46.7% to 100%) and low percentages of false positives (mean:  $14.6\% \pm 2.4\%$ SE, range: 6.7% to 19.5%). Further CART analysis of differences between occupied sites based on relative occurrences did not produce valid models.



**Figure 5.9** Percentage contribution of the presence of *M. latifrons* in each group relative to the total number of presences across all groups per trip ( $\pm$ SE) for the training data and test trips

### 5.3.5 Overlap in spatial patterns

There was a substantial overlap in predicted spatial distribution patterns for species belonging to the same taxonomic group, but little overlap between the taxonomic groups (Table 5.1). For example, *U. seismella* occurred 10 times more often in the predicted high occurrence cluster of *U. coarctata* than in the sites predicted to be occupied by *M. frontalis*. Moreover, *U. seismella* was absent from sites predicted to be occupied by *M. latifrons*. By contrast, sites with predicted occurrence of *M. latifrons* were completely contained within sites with predicted occurrence of *M. frontalis*, but shared little overlap with the predicted spatial distribution of *U. coarctata*.

**Table 5.1** The average percentage of sites ( $\pm$ SE) per species that overlap into the predicted high occurrence cluster of *U. coarctata* and sites predicted to be occupied by *U. seismella*, *M. frontalis* and *M. latifrons*

	<i>U. coarctata</i>	<i>U. seismella</i>	<i>M. frontalis</i>	<i>M. latifrons</i>
<b>High occurrence cluster” of <i>U. coarctata</i></b>		77.0% $\pm$ 8.3%SE	33.6% $\pm$ 5.6%SE	11.7% $\pm$ 1.7%SE
<b>Sites occupied by <i>U. seismella</i></b>	29.0% $\pm$ 3.1%SE		8.0% $\pm$ 1.2%SE	0.0% $\pm$ 0.0%SE
<b>Sites occupied by <i>M. frontalis</i></b>	11.4% $\pm$ 1.9%SE	7.2% $\pm$ 1.0%SE		42.5% $\pm$ 5.0%SE
<b>Sites occupied by <i>M. latifrons</i></b>	9.4% $\pm$ 1.4%SE	0.0% $\pm$ 0.0%SE	100% $\pm$ 11.8%SE	

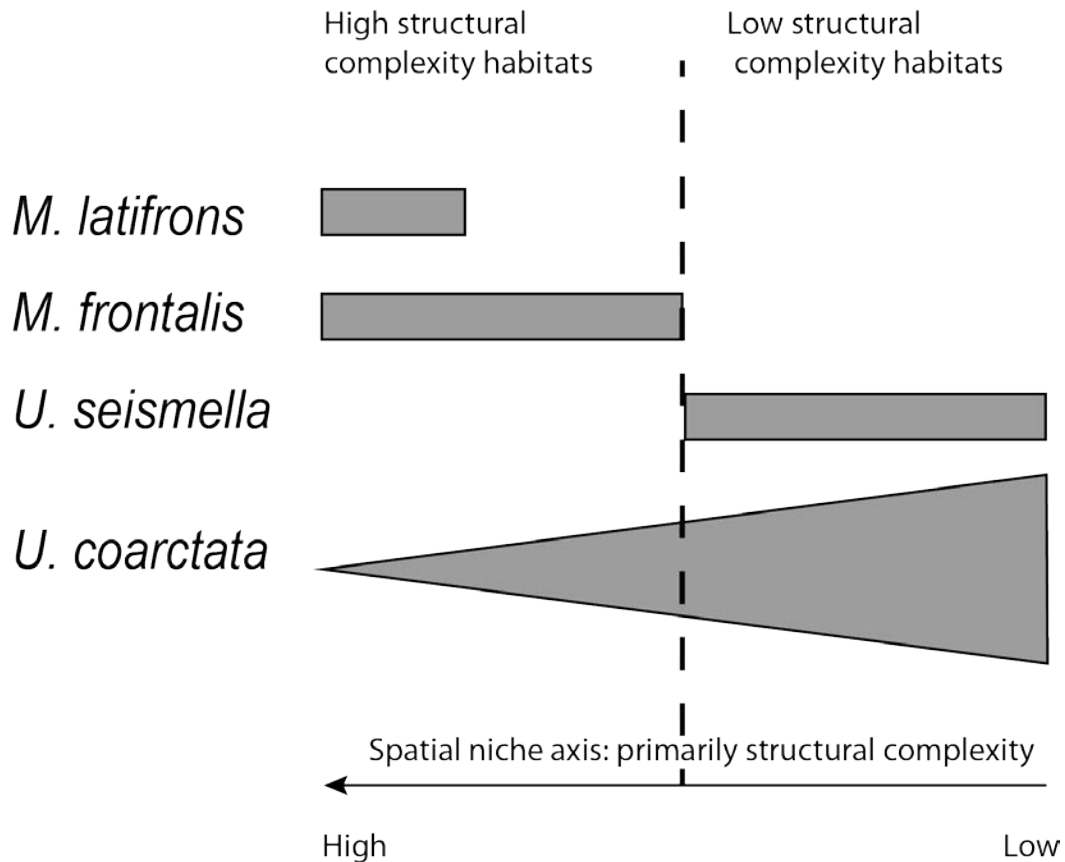
## 5.4 Discussion

Distinct, temporally stable crab/habitat associations were found for four species, supporting the niche-assembly theory in which spatial distribution patterns are created by interactions with the biotic and abiotic environment, as the main mechanism structuring spatial distribution patterns within tropical estuaries, rather than mechanisms that are neutral to the environmental landscape, such as dispersal, chance and history (Potts et al., 2004, Gilbert et al., 2008). Habitat association models identified clusters of sites with distinct environmental characteristics based on occurrence of intertidal crabs. This is in agreement with previous studies that found strong associations between crabs and environmental factors at site or transect specific scales (Weis and Weis, 2004, Koch et al., 2005, Arruda Bezerra et al., 2006, Ravichandran et al., 2007, Takeda, 2010). Additionally, the observations of intertidal crab occurrence patterns generally fitted well with the predictions of the habitat association models. For example, within-site occurrence patterns were stable for *U. coarctata* except for the dry season in 2009 and 2011 (Fig. 5.5). However, light rainfall and very low tides could have influenced the data sampled at these times, because they could have impacted on the surface activity patterns (Kyomo, 1986) or result in small movements towards the low water mark (Colby and Fonseca, 1984, Gherardi and Russo, 2001) respectively. Similarly, high sensitivities of the within-estuary occurrence models of *U. seismella*, *M. frontalis* and *M. latifrons* suggest accurate

identification of sites where the species were present. Meanwhile, low false positive rates across all trips for the latter three species indicate high probability of observing species within their predicted habitats. In conclusion, for the first time, a predictable pattern of spatial distribution of intertidal crabs in distinct habitats within the large spatial context of the estuarine landscape was demonstrated.

The identification of distinct habitats allows for the formulation of a conceptual model of spatial distribution patterns of intertidal crabs in relation to the environmental landscape of tropical estuaries (Fig. 5.10). This model was developed using the calculated overlaps in the spatial distribution predicted by the individual habitat association models of the four species. In particular, the presence/absence models of *M. frontalis*, *M. latifrons* and *U. seismella* and the relative occurrence model of *U. coarctata* were used. Because of the low overlap in predicted spatial distribution patterns for species belonging to different taxonomic groups, *Metopograpsus* spp. and *Uca* spp. occur at opposing ends along a spatial niche axis. Additionally, *M. frontalis* and *M. latifrons* associated with sites characterized by high structural complexity, while *U. seismella* occupied sites characterized by low structural complexity. Consequently, one of the main niche axes that underlie the spatial pattern is a gradient in structural complexity. In contrast to previous studies which predominantly focused on small site or transect specific scales (Koch et al., 2005, Arruda Bezerra et al., 2006, Takeda, 2010), this conceptual model displays habitat associations at a landscape scale and allows for a simple visualization of the main trends in spatial organization of intertidal crab assemblages at this scale.





**Figure 5.10** Conceptual model of the patterns of spatial organization of intertidal crab assemblages within a tropical estuary based on the predictions for the four individual species models. Rectangles are presence/absence models and the triangle is based on the relative occurrence model of *U. coarctata*. Species are organized along a spatial niche axis, which in this case is strongly driven by changes in structural complexity

A large overlap in spatial distribution patterns was predicted for species belonging to the same taxonomic group, but little overlap between taxonomic groups (Table 5.1). The presence of distinct communities of *Uca* spp. and *Metopograpsus* spp. supports the community continuum concept (Whitaker, 1975) more than Gleason's (1926) individualistic continuum concept (Austin, 1985). Additionally, the occurrence of separate niches for different genera demonstrates a distinct spatial organization of intertidal crab communities in an area previously considered homogeneous (Lee, 2008). Because *Uca* spp. and *Metopograpsus* spp. perform different ecosystem functions (Kristensen, 2008), the existence of taxon-specific niches has fundamental implications for the diversity and

spatial distribution of ecosystem services mediated by intertidal crabs across the low intertidal zone.

The clear taxonomic organization of the communities is likely related to greater similarity in adaptations to the physical environment of intertidal crab species within rather than among taxonomic groups. For instance, the association of *Metopograpsus* spp. with structure is related to their need for shelter among roots and logs (Cannicci et al., 1999) and their feeding on macro-algae that grow on hard substrata (Sivasothi, 2000, Shaw and Tibbetts, 2004, Poon et al., 2010). By contrast, because of their sediment feeding (Bouillon et al., 2002, Meziane et al., 2002), their burrowing behavior (Kristensen, 2008) and visual communication (Hemmi et al., 2006, How et al., 2008), *Uca* spp. are less dependent on structure and might even avoid it. In conclusion, the conceptual model of spatial distribution patterns provides a framework to place previous, small scale, knowledge into a landscape level scale where many fundamental estuarine ecosystem processes are working, where effects of climate change and urbanization are operating and where environmental management is often focused.

This study does not provide a complete ecological understanding of spatial distribution patterns of intertidal crab communities within the low intertidal zone of tropical estuaries. For instance, despite their presence in Stuart Creek (Fig. 5.3) no valid models for the habitat associations of *M. japonicus*, *U. dussumieri* and *U. signata* could be made. High densities of *U. signata* have been reported on salt pans (Rabalais and Cameron, 1985, Nobbs, 2003), and of *M. japonicus* on low intertidal mudflats (Snelling, 1958, Hawkins and Jones, 1982, Jones and Greenwood, 1982, Otani et al., 2010). Salt pans are available higher in the intertidal of Stuart Creek and mudflats are available at the mouth of Ross River estuary. Consequently, the within-estuary occurrence of these species could be a result of a spillover from these habitats, meaning that their occurrence may be influenced by spatial variables at tidal levels not considered in this study. Additionally, the low within-estuary occurrence of *U. dussumieri* could be due to a preference for silt sediments (Sasekumar, 1974, Weis and Weis, 2004), potentially finer than those found in Stuart Creek. Furthermore, some species occupying the low intertidal zone are rarely represented using photography (Chapter 3). Nonetheless, the position of these species in the spatial model and the ecological implications of their habitat associations deserve

attention as they can reach high densities (Chapter 3). Additionally, using the photographic technique there is a small potential for mis-identification of species. This issue was addressed in this thesis by the collection of voucher specimens (during work for Chapters 2 and 3) which could be exactly identified and compared to crabs observed in the photographic samples hence avoiding systematic mis-identification. Furthermore, accidental mis-identification of unique individuals is unlikely to have had a major influence on the overall outcomes of analysis because of the large number of replicate samples for each trip and the strong taxonomic patterns observed. Finally, the model proposed here is applicable to the location where it was developed. Consequently, its relevance to other systems needs to be validated. Nonetheless, within the constraints within which the model was developed, the study provides a first insight in the predictability and patterns of habitat association of crabs occupying the low intertidal zone.

# Chapter 6: Converting the conceptual model to an ecological model of intertidal crab habitat associations applicable across estuaries

## 6.1 Introduction

Intertidal crabs are highly abundant components of tropical estuaries that are intimately connected to many other organisms and key ecological processes through their roles in trophic transfer and ecosystem engineering (Angsupanich and Aksornkoe, 1996, Apel and Tuerkay, 1999, Amaral et al., 2009). This ecological connectivity is particularly extensive in the low intertidal zone because regular tidal inundation enables connectivity between the resident crab fauna and transient estuarine components (Cannicci et al., 1996b, Botto et al., 2000, Sheaves and Molony, 2000). Consequently, changes in estuarine assemblages or functions are likely to be reflected in intertidal crab assemblages, and changes in the latter are likely to impact on other estuarine components and functions. Hence knowledge of the ecology of intertidal crabs is fundamental to the understanding of many important estuarine ecosystem processes. However, integration of intertidal crabs in models of estuarine processes has been hampered by a lack of a broadly applicable ecological model of their spatial distribution patterns within and across estuarine habitat landscapes (Chapter 1).

A conceptual model of distinct, temporally stable habitat associations of four intertidal crab species was developed within one tropical estuary (Chapter 5). This model outlined the low intertidal zone as a heterogeneous habitat landscape occupied by communities with unique taxonomic identities. In particular, *Uca* spp. occupied habitats characterized by low structural complexity, while *Metopograpsus* spp. associated with habitats with high structural complexity (Chapter 5). Additionally, in combination with previous research that demonstrated strong associations between intertidal crabs and environmental parameters (Weis and Weis, 2004, Koch et al., 2005, Arruda Bezerra et al., 2006, Ravichandran et al., 2007, Takeda, 2010), the model suggests that niche assemblages are primary mechanisms creating the spatial distribution patterns of intertidal crabs. Both the spatial

pattern of intertidal crab communities and the niche association mechanisms underlying it affect the diversity and stability of ecological services provided by intertidal crabs (Chapter 5). However, because most research on spatial distribution patterns of intertidal crabs has focused on single estuaries, the applicability of this knowledge across estuaries is unknown.

A few studies have addressed spatial distribution patterns across estuaries. For instance, a common spatial distribution pattern was established between the families Grapsidae and Sesarmidae and mangrove trees using five transects across two estuaries 140km apart (Dahdouh-Guebas et al., 2002). However, in this case differences between estuaries or sites were not addressed (Dahdouh-Guebas et al., 2002). Consequently, the predictability of Grapsidae and Sesarmidae spatial distribution relative to mangrove tree spatial distribution across estuaries remains unquantified. Likewise, relative numbers of crabs from the superfamilies Ocypodoidea and Grapsoidea in floristically similar sites between two estuaries were comparable for each of four locations along the East African Coast (Hartnoll et al., 2002). Although this similarity in numbers indicates predictability in abundance between comparable sites, the limited taxonomic resolution (superfamily level only) provides little information on species composition. In conclusion, it is not known whether the pattern of spatial distribution within estuaries is comparable across different estuaries and whether there are predictable similarities or differences between estuaries. Nonetheless, this knowledge is crucial to understand the transferability of ecological knowledge from one estuary to another and to gain an improved knowledge of the processes structuring intertidal crab assemblages within and across estuaries.

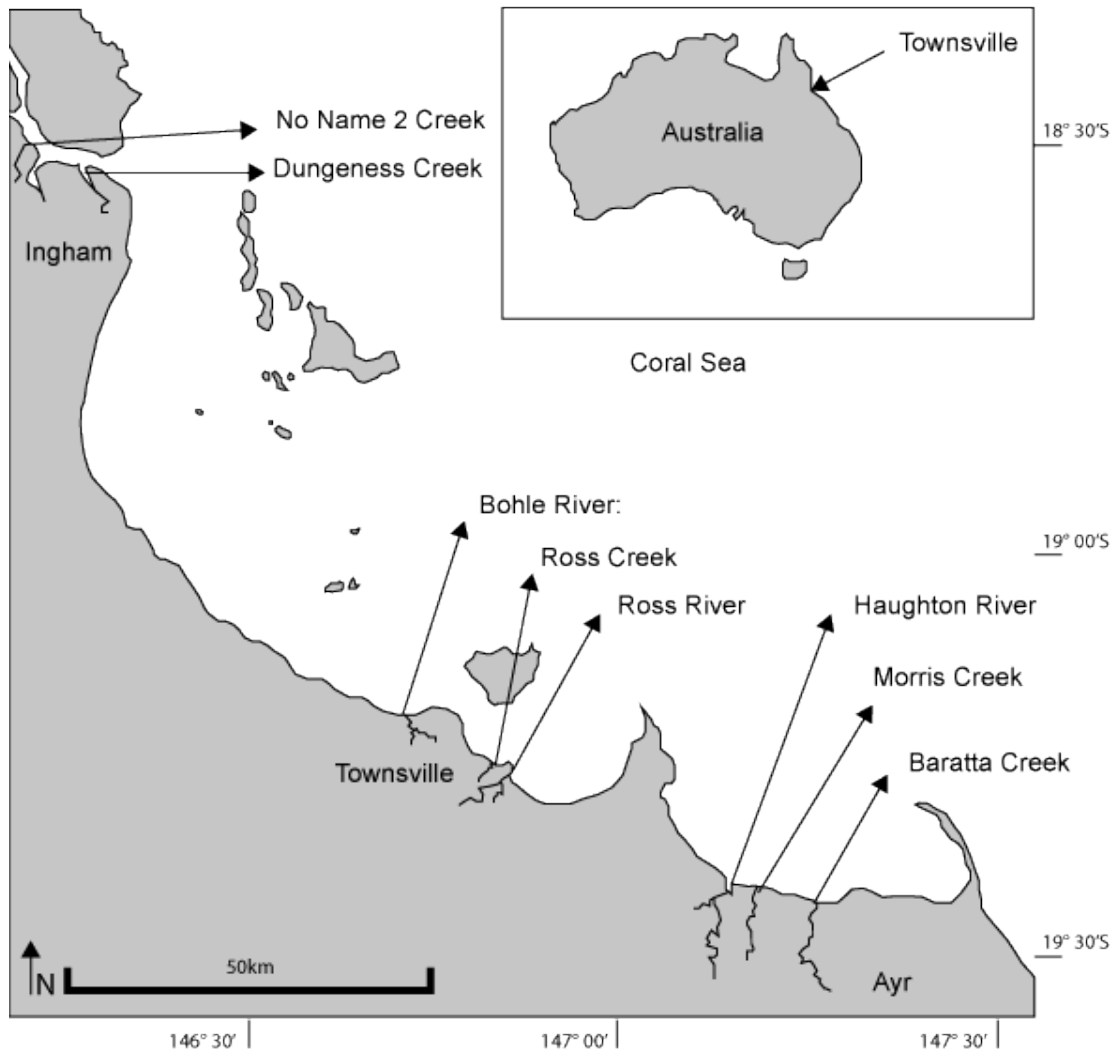
The aim of this chapter is to provide a formal landscape level spatial framework needed to integrate the role of intertidal crabs into large scale, within and among estuarine ecosystem process-models. Therefore, the conceptual model of intertidal crab spatial organization patterns constructed in Chapter 5 is further developed and tested using predictive habitat association modeling of individual intertidal crab species within and across estuaries, to produce a generally applicable ecological model of spatial organization of intertidal crab assemblages within and among estuaries.

## 6.2 Methods

### 6.2.1 Study area

Sampling was conducted in eight dry tropical estuaries over 160 km in North Queensland, Australia (Fig. 6.1). The estuaries are characterized by high seasonal rainfall, with nearly 80% of the average annual rainfall of 1149.9mm occurring during the summer wet season, December to March (Bureau of meteorology, data for Townsville between 1940 and 2011). Sampling was conducted in the post wet (April to May) and pre wet (September to October) season of 2009 and 2010. Total annual rainfall in these years was high (1989.4mm and 2006.4mm respectively, Bureau of Meteorology). Consequently, salinities, particularly in the larger estuaries (Baratta River, Bohle River and Morris Creek), were at times lower than local seawater levels of about 35‰. The estuaries have semidiurnal tides with tidal ranges around 3m on spring tides. Lowest spring tides occur during the day in the dry season and at night in the wet season.

The low intertidal zone within the eight estuaries was characterized by a diversity of morphological features. The angle of the sediment surface ranged from horizontal to vertical. Four classes of vegetation bordered the low intertidal zone: 1) mangrove vegetation growing between mean sea level and mean high water at neap tide including *Rhizophora stylosa*, *Avicennia marina* and *Aegiceras corniculatum* (hereafter referred to as low intertidal vegetation); 2) mangrove vegetation above mean high water at neap tide, predominantly *Ceriops* spp. and *Burquiera gymnorhiza* (hereafter referred to as high intertidal vegetation); 3) grasses growing above mean high water at neap tide, chiefly *Sporobolus virginicus* and 4) bare banks, devoid of intertidal vegetation. Different structural elements were present, including fallen timber, grass clumps, pneumatophore roots, prop roots, cable roots and buttress roots. Very fine sand to silt aggregates dominated the sediment grain sizes based on the Udden-Wentworth classification (Wentworth, 1922). However, some sandy patches were present and rubble and rock walls occurred in human modified areas of Ross Creek, Ross River and Baratta Creek Downstream.



**Figure 6.1** Location of estuaries studied

### **6.2.2 Sample collection**

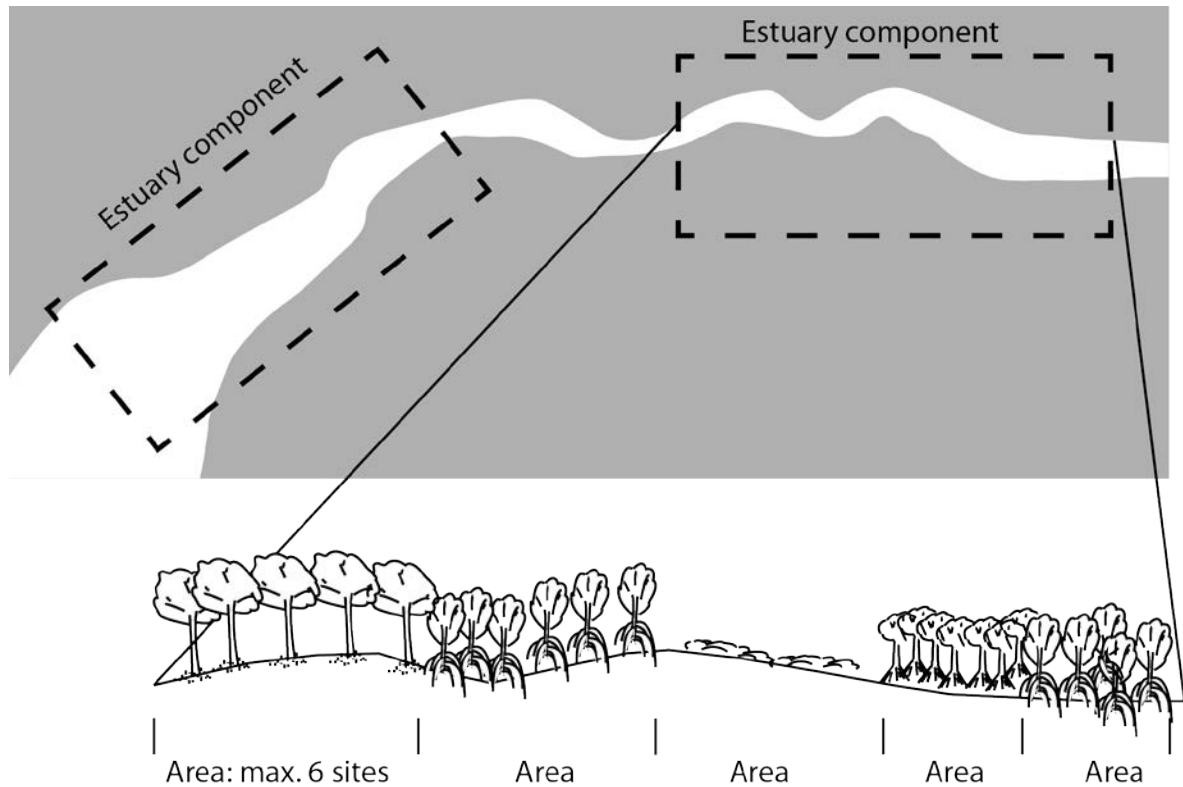
Estuaries were divided into components (Table 6.1, Fig. 6.2) to allow different arms and up- and downstream parts of estuaries to be studied separately. The whole low intertidal zone within each component was then divided in areas, based on changes in dominant vegetation (Fig. 6.2). A maximum of six sites, 15 to 20m long and 10m apart, were then randomly selected within each area, depending on its size. This sampling strategy was chosen to maximize representation of the environmental heterogeneity along the low

intertidal zone. Vegetation was chosen to identify areas because it has previously been associated with intertidal crab distribution (Dahdouh-Guebas 2002) and because it allows for a clear division in areas with different structural heterogeneity. The 10m between sites ensured that sites were spatially independent of each other, because adult intertidal crabs have home ranges restricted to a few square meters (Cannicci, 1996a, 1999, Zeil and Henmi, 2006).

**Table 6.1** Sampling times and estuaries, including components and the number of sites sampled within them

<b>Estuary</b>	<b>Components</b>	<b>Sampling period</b>	<b>No. of Sites</b>
<b>No Name 2 Creek</b>	No Name 2 Creek	Pre wet 2009	51
<b>Dungeness Creek</b>	Dungeness Creek	Pre wet 2009	53
<b>Bohle River</b>	Bohle Downstream	Post wet 2009, Pre wet 2010	77, 70
	Bohle East Upstream Arm	Pre wet 2010	46
	Bohle West Upstream Arm	Pre wet 2010	45
<b>Ross Creek</b>	Ross Creek	Post wet 2010	40
<b>Ross River</b>	Ross River	Post wet 2009	58
	Stuart Creek	Post wet 2009	54
<b>Houghton River</b>	Houghton River	Post wet 2009	58
	Doughboy Creek	Post wet 2009	80
<b>Morris Creek</b>	Morris Downstream	Pre wet 2010	47
	Morris Upstream	Pre wet 2010	54
<b>Baratta Creek</b>	Baratta Downstream	Pre wet 2010	62
	Baratta Upstream	Pre wet 2010	73





**Figure 6.2** Schematic overview of the sampling design used, with indication estuarine components and areas, selected based on changes in vegetation, within the low intertidal zone of these components

Presence or absence of intertidal crab species within each site was established using photography following the protocol developed in Chapter 3. Additionally, morphological factors outlining the environment within each site, including: canopy overhang, bank angle, vegetation class, substratum and amount of logs, pneumatophores, grass, prop roots, other roots and structure were sampled using the methods described in Chapter 5. One day of sampling was conducted per component during ebb of spring tides, with low tide between 12am and 3pm. This consistent timing was chosen to reduce potential effects of variable surface activity patterns over different temperature and humidity levels across the day on sampling (Chapter 4).

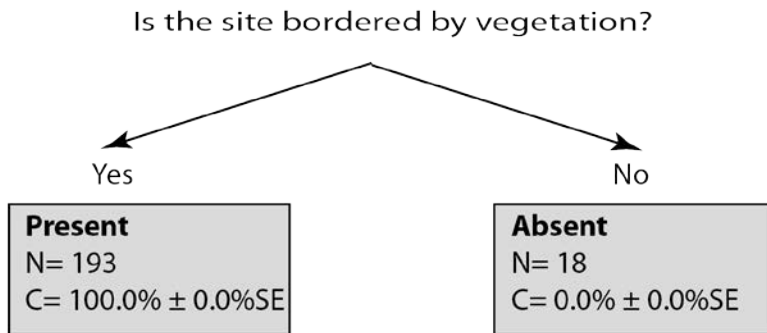
### **6.2.3 Statistical analysis**

Predictive habitat modeling was used to cluster sites into habitats for individual species (Guisan and Zimmermann, 2000). Classification and regression tree analyses (CART, De'ath, 2002), using presence-absence within-site data as the categorical dependent, underpinned the habitat models as described in Chapter 5. Vegetation class and substratum were the categorical predictors and bank angle, canopy overhang and average percentage of logs, grass, pneumatophores, prop roots, other roots and structure covering the substratum at the site level were continuous variables. Models were constructed using the data from Bohle River Downstream, Doughboy Creek, Houghton River, Ross River and Stuart Creek as the training data, and the other systems as individual model tests. Bohle River Downstream was sampled both in post wet 2009 and in pre wet 2010 and was included as both a model and test respectively. This repeated sampling was conducted to check if spatial distributions within one system were stable over time as proposed in Chapter 5. The predictive ability of the models was assessed with sensitivity analyses, calculating the sensitivity and percentage of false positives. Sensitivity quantifies the number of sites observed with the species present that were predicted as having the species present. The percentage of false positives is the percentage of sites which were predicted as occupied by a species, but where the species was observed to be absent. Models with high sensitivity and low percentages of false positives were preferred because they allowed precise classification of sites with a high probability of finding the organism present. Finally, the predicted spatial presence and overlap between spatial distribution patterns were compared by analyzing the number of sites where a species was predicted to occur, and the number of sites where species were predicted to co-occur relative to the total number of sites.

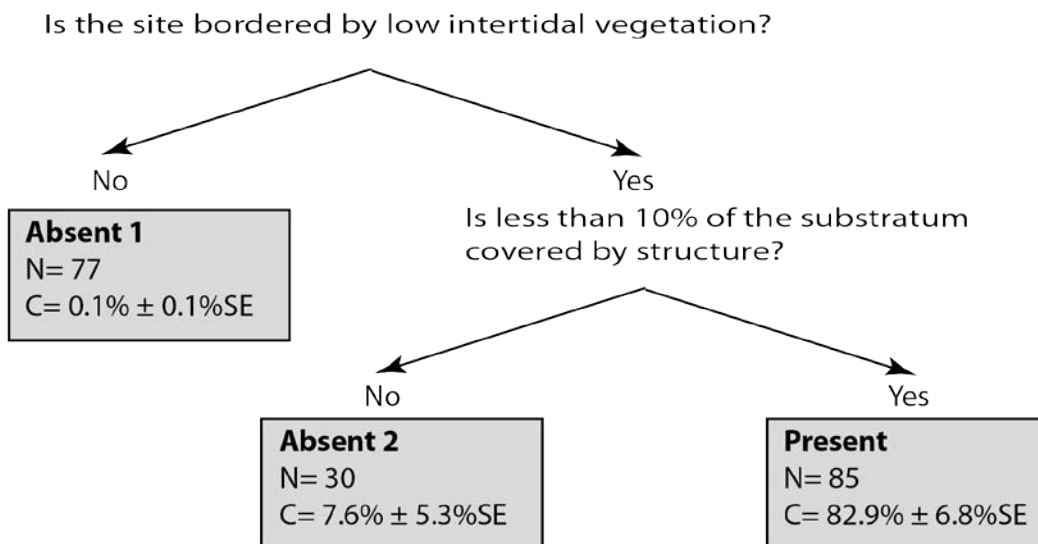
## 6.3 Results

Individual species habitat-association models could be developed for six out of nine species recorded throughout the study (Fig. 6.3). All models were based on CART analyses, except the *M. frontalis* model, where the CART model was amended based on field observations and previous literature (Appendix 4.3). Valid models could not be developed for *U. signata*, *U. dussumieri* and *U. vomeris*, likely due to their low presence across sites. *U. coarctata* was predicted to occupy sites bordered by any type of vegetation (Appendix 4.1). *U. seismella* had a more restricted distribution and was predicted to occupy sites bordered by low intertidal vegetation with less than 10% of the substratum covered by structure (Appendix 4.2). *M. japonicus* was predicted to occupy muddy sites with bank angles less than 40°, no canopy overhang and less than 48% of the substratum covered by pneumatophores. *M. frontalis* and *M. latifrons* were predicted to occupy sites where the substratum was covered by structure for more than 10% and 25% respectively. Additionally, all *Metopograpsus* spp. were predicted to occupy sites with rock-walls.

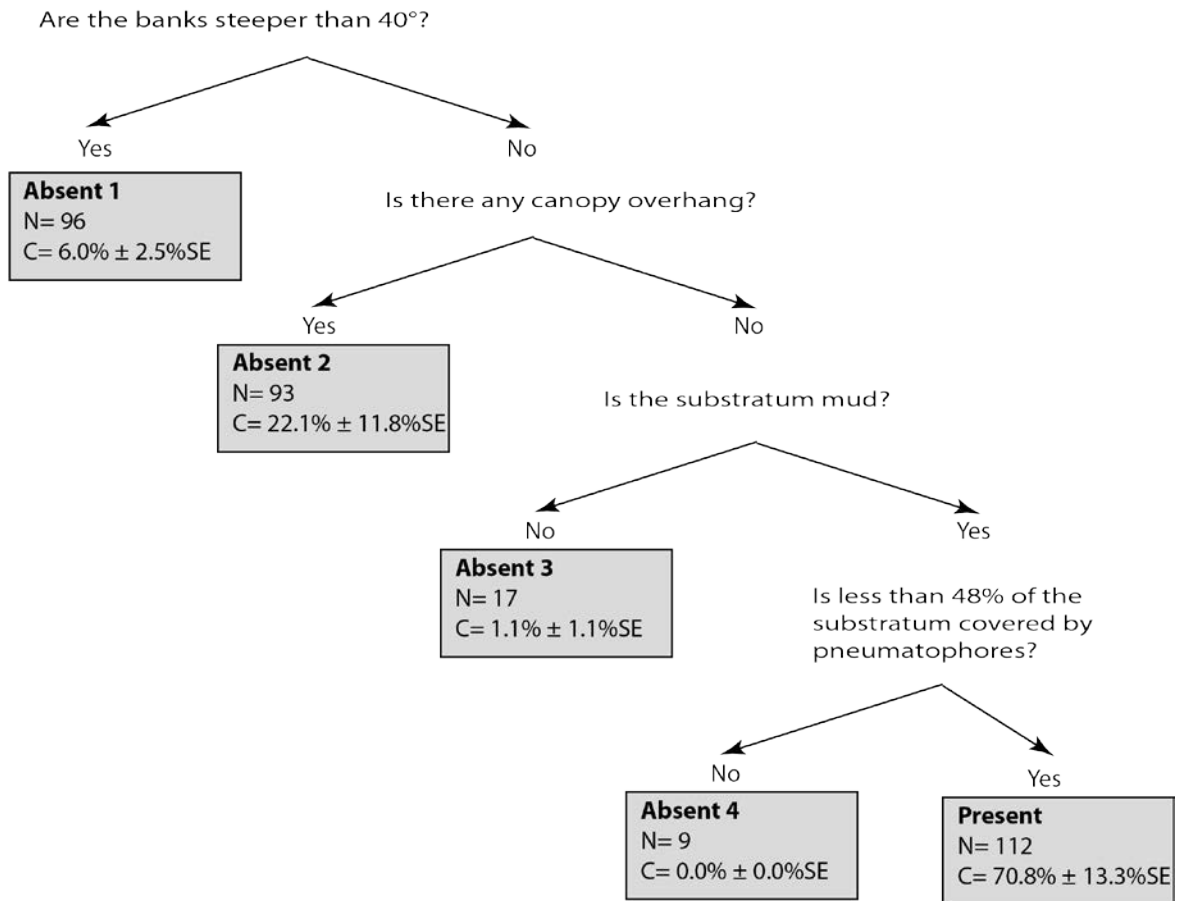
*U. coarctata*



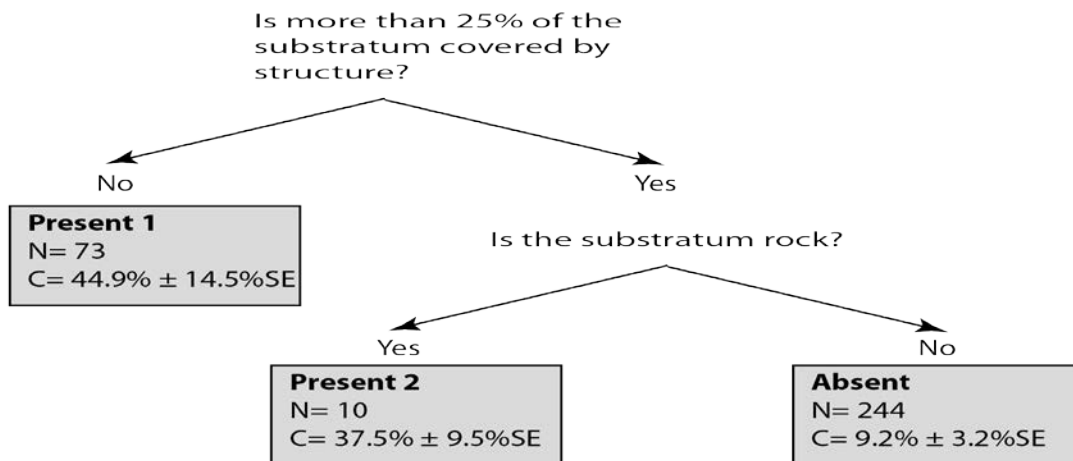
*U. seismella*



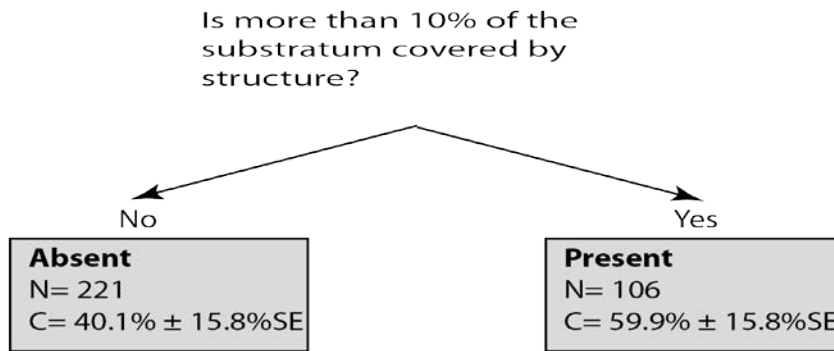
*M. japonicus*



*M. latifrons*

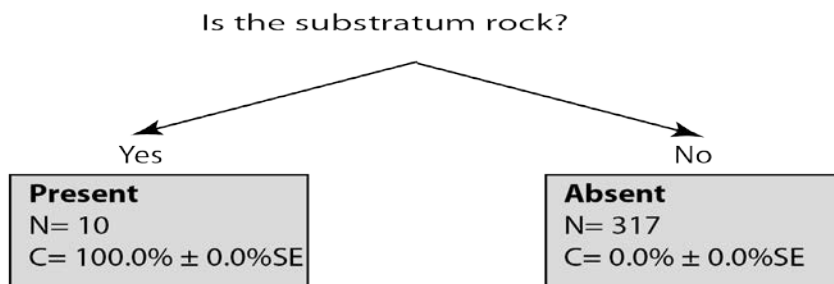


***M. frontalis***



**Note: all sites with rock-substratum are also categorized under the Present cluster**

***M. thukuhar***



**Figure 6.3** CART models of habitat-association for individual species, based on presence-absence within site data, with indication of the number of sites (N) within each group of sites and the average percentage (C) of occurrences of each species within each group across the model estuaries

Overall, the predictive abilities of the individual species models across test estuaries showed moderate to high sensitivity (Table 6.2) and low percentages of false positives (Table 6.3) for observations in sites predicted to be occupied sites versus those predicted to be unoccupied. An exception was the generally high percentage of false positives recorded for the model of *U. coarctata*. The sites predicted as occupied by the CART for this species included almost all sites. Although the habitat that *U. coarctata* associates with is likely to fall among these sites, the high percentage of false positives indicates that

a finer description of the occupied sites of *U. coarctata* is needed. However, this was not possible with the variables used in this study. By contrast, the occupied sites of *M. latifrons* were defined too narrowly as evidenced by the low sensitivity observed for the model of *M. latifrons*. However, since the percentage of false positives observed for *M. latifrons* were low, observations of *M. latifrons* within occupied sites were almost certain. Overall, the models delineated the core habitats of the six species with high accuracy.

**Table 6.2** Sensitivity recorded for individual species habitat-association models in the test systems, (-) Indicates systems that could not be tested for that species, species are: *U. c.*: *Uca coarctata*, *U. s.*: *Uca seismella*, *M. j.*: *Macrophthalmus japonicus*, *M. f.*: *Metopograpsus frontalis*, *M. l.*: *Metopograpsus latifrons* and *M. t.*: *Metopograpsus thukuhar*

	<i>U. c.</i>	<i>U. s.</i>	<i>M. j.</i>	<i>M. f.</i>	<i>M. l.</i>	<i>M. t.</i>
<b>Baratta Downstream</b>	97.1	40	68.8	53.1	60	100
<b>Baratta Upstream</b>	100	72.7	50	62.5	38.5	-
<b>Bohle River</b>	100	60	38.9	52.6	28.2	-
<b>Bohle West Upstream arm</b>	100	38.5	75	50	20	-
<b>Bohle East Upstream arm</b>	100	73.3	19	28.6	3.4	-
<b>Dungeness</b>	100	57.1	100	81.8	82.4	-
<b>Morris downstream</b>	90.6	45	68.8	60.7	58.3	-
<b>Morris upstream</b>	93.9	94.1	50	54.8	30	-
<b>No Name 2 Creek</b>	100	71.4	90.9	93.3	60	-
<b>Ross Creek</b>	92.3	100	-	90.5	100	100
<b>Average</b>	<b>97.4</b>	<b>65.2</b>	<b>62.4</b>	<b>62.8</b>	<b>48.1</b>	<b>100</b>
<b>St Err</b>	<b>1.2</b>	<b>6.7</b>	<b>8.1</b>	<b>6.4</b>	<b>9.3</b>	<b>0</b>

**Table 6.3** Percentages of false positives recorded for individual species habitat-association models in the test systems, (-) Indicates systems that could not be tested for that species, species are: *U. c.*: *Uca coarctata*, *U. s.*: *Uca seismella*, *M. j.*: *Macrophthalmus japonicus*, *M. f.*: *Metopograpsus frontalis*, *M. l.*: *Metopograpsus latifrons* and *M. t.*: *Metopograpsus thukuhar*.

	<i>U. c.</i>	<i>U. s.</i>	<i>M. j.</i>	<i>M. f.</i>	<i>M. l.</i>	<i>M. t.</i>
<b>Baratta Downstream</b>	25.9	14.8	33.3	0	0	0
<b>Baratta Upstream</b>	100	48.4	15.5	4.1	3.3	-
<b>Bohle River</b>	29.4	10	32.4	12.5	0	-
<b>Bohle West Upstream Arm</b>	33.3	3.1	7.3	32	10	-
<b>Bohle East Upstream Arm</b>	100	41.9	8	0	0	-
<b>Dungeness Creek</b>	100	30.4	6	52.4	30.5	-
<b>Morris downstream</b>	73.3	14.8	16.1	5.3	11.4	-
<b>Morris upstream</b>	80	13.5	11.9	8.7	2.3	-
<b>No Name 2 Creek</b>	55.2	11.4	27.5	36.1	7.7	-
<b>Ross Creek</b>	51.9	64.1	85	21.1	23	52.8
<b>Average</b>	<b>64.9</b>	<b>25.2</b>	<b>24.3</b>	<b>17.2</b>	<b>8.8</b>	<b>26.4</b>
<b>St Err</b>	<b>9.5</b>	<b>6.3</b>	<b>7.5</b>	<b>5.6</b>	<b>3.3</b>	<b>11.8</b>

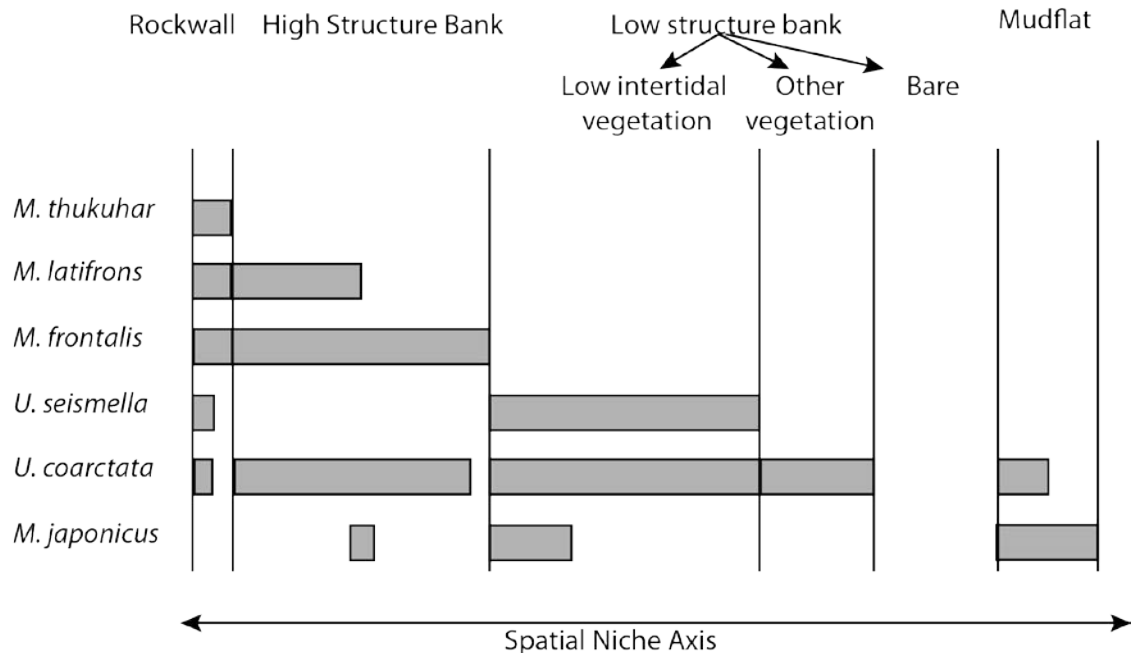
High overlap in spatial distribution patterns were predicted within superfamilies Ocypodoidea and Grapsoidea, but little between them. Due to the broad range of sites where *U. coarctata* was predicted to occur, there were large overlaps between this species and predicted spatial distributions of all other species (Table 6.4). However, if *U. coarctata* is omitted from consideration, the greatest overlap occurred among *Metopograpsus* spp., and among *U. seismella* and *M. japonicus*. Additionally, sites predicted to be occupied by *M. thukuhar* and *M. latifrons* overlapped completely with parts of the predicted occupied sites of *M. frontalis*. Similarly, sites with predicted occurrence of *U. seismella* overlapped completely with parts of the predicted occupied sites of *U. coarctata*. Using these percentages of overlap, the predicted spatial distribution patterns of the different species can be compared relative to each other.



**Table 6.4** Percentages of overlap in predicted spatial distributions of species across all test systems, species are: *U. c.*: *Uca coarctata*, *U. s.*: *Uca seismella*, *M. j.*: *Macrophthalmus japonicus*, *M. f.*: *Metopograpsus frontalis*, *M. l.*: *Metopograpsus latifrons* and *M. t.*: *Metopograpsus thukuhar*.

	<i>M. f.</i>	<i>M. l.</i>	<i>M. t.</i>	<i>M. j.</i>	<i>U. s.</i>	<i>U. c.</i>
<i>M. frontalis</i>		21.8	5.5	2.4	1.7	33.8
<i>M. latifrons</i>	21.8		5.5	1.5	1.7	17.9
<i>M. thukuhar</i>	5.5	5.5		0	1.7	1.7
<i>M. japonicus</i>	2.4	1.5	0		10.9	17.4
<i>U. seismella</i>	1.7	1.7	1.7	10.9		35.3
<i>U. coarctata</i>	33.8	17.9	1.7	17.4	35.3	
<b>Total predicted presence</b>	37.7	21.8	5.5	25.5	35.3	86.5

Combining the individual species habitat-association models and the overlap between the predicted spatial distributions allows a broad ecological model of intertidal crab assemblages along a spatial niche axis to be developed (Fig. 6.4). This model outlines six habitats, each with distinct assemblages. *Metopograpsus* spp. are all predicted to occupy sites with rock walls and are thus a distinct assemblage that outlines rock walls as a habitat. Additionally, *M. frontalis* and *M. latifrons* associate with sites on structurally complex banks and thus identify this as a habitat. By contrast the predicted habitat association of *U. seismella* outlines banks with little structural complexity, bordered by low intertidal vegetation, as a distinct habitat, and the presence of *M. japonicus* identifies sites consisting of flat mud areas with little vegetation influence, which can broadly be identified as a mudflat habitat. Sites where *U. coarctata* is predicted to occur alone are identified as low structure banks with any vegetation except the low intertidal vegetation already described as the habitat of *U. seismella*. Finally, there are some sites where no species are predicted to occur. These are identified as bare, low structure habitats.



**Figure 6.4** An ecological model of broad habitats of intertidal crabs occupying the low intertidal zone, based on individual species habitat-association models

## 6.4 Discussion

Predictable habitat associations of intertidal crabs were established within and across estuaries, demonstrating that the pattern of spatial distribution of intertidal crab within estuaries is comparable across estuaries. The modeled habitat associations of six intertidal crab species outlined core habitats of these species with moderate to high sensitivity and low percentages of false positives across independent test estuaries. The main exception is *U. coarctata*. This species is a spatial generalist species (Chapter 5), which could explain why the presence-absence data used to develop the habitat association model delineated a large area as potential habitat for this species. This large delineation of the potential habitat lies at the basis of the high sensitivity recorded for this species across test estuaries. However, the preferred habitat of *U. coarctata*, as demonstrated by high densities, falls in areas with low structural complexity (Chapter 5). This could explain why a large percentage of false positives was observed for the predicted distribution of *U. coarctata*. Thus, the model of *U. coarctata* needs further refinement. Likewise, the habitat-association models of the other species could benefit

from further refinement, for instance, to improve the overall low sensitivity of the habitat-association model of *M. latifrons*, or to reduce the variability in predictions of the model of *M. thukuhar* across systems. Nonetheless, despite small inaccuracies, the models developed in this study allow for the delineation of predictable habitat-associations within and across tropical estuaries, using simple morphological parameters. Although simple and reductionist in nature, the models form the basis for an improved understanding of the patterns and processes structuring spatial distribution patterns at these scales and provide a first insight in the transferability of knowledge on spatial ecology of intertidal crabs across estuaries.

A model of the spatial distribution of intertidal crab assemblages (Fig. 6.4), constructed using the calculated overlap in predicted spatial distribution and the similarities in habitat-association of the individual species, supports and expands the notion that the low intertidal zone contains a heterogeneous habitat landscape of taxonomic clusters (Chapter 5). Although the predicted spatial distribution of *U. coarctata* appears to overlap across all habitats, the core habitat, as discussed in the previous paragraph, likely lies within areas of low structural complexity. Similarly, *U. seismella* is predicted to occur in some areas with rock walls. However, they are not the dominant species here in terms of number of sites occupied. Additionally, given the very different environmental conditions on rock walls compared to areas with low structural complexity that are bordered by low intertidal vegetation, in which *U. seismella* occupies nearly all sites, it is unlikely that this species would reach high densities and thus contribute significantly to the ecosystem functioning of the intertidal crab assemblage on rock walls. For similar reasons, the overlap of *M. japonicus* in some non mudflat areas is unlikely to have a substantial influence on ecosystem services provided by the intertidal crab assemblage in these habitats. In conclusion, unique habitats in the low intertidal zone are designated by distinct assemblages with a strong taxonomic identity. These assemblages are formed by tight habitat associations, matching with previous research indicating strong relationships between crabs and environmental parameters (Weis and Weis, 2004, Koch et al., 2005, Arruda Bezerra et al., 2006, Ravichandran et al., 2007, Takeda, 2010) and supporting the niche theory as primary mechanism driving spatial distribution patterns of intertidal crabs within tropical estuaries (Chapter 5).

Although the ecological model does not provide direct information regarding the factors underlying spatial distribution patterns, it does allow the importance of potential gradients to be assessed and presents an ecological framework of realized spatial niches in which to place previous, site or transect specific knowledge regarding specific factors affecting spatial distribution patterns of intertidal crabs (Arruda Bezerra et al., 2006, Lim and Heng, 2007, Ravichandran et al., 2007, Takeda, 2010). For example, factors relating to a structural gradient appear influential at a broad level because they reflect the dominant taxonomic split between habitat-associations of intertidal representatives of the superfamilies Grapsoidea and Ocypodoidea. Meanwhile, at finer levels, factors associated with the presence of vegetation separate species within the Ocypodoidea. In conclusion, the broad ecological model provides a formal statistical formulation of intertidal crab spatial distribution patterns at landscape scales, as an alternative to the predominantly site- or transect-specific views of intertidal crab spatial ecology.

One way of using this statistical understanding to advance research of spatial ecology is by using it as a hypothesis. For instance, no false positives were observed for *M. thukuhar* in the Baratta Downstream system, which is characterized by rock-walls made of boulder aggregations. By contrast, half of the predicted occurrence sites of *M. thukuhar* were observed as absent in Ross Creek, which is characterized by a variety of rock-wall types. Hence, testing of the ecological model quickly indicated that the designation of rock walls needs to be revisited and that Ross Creek could provide the necessary landscape to do so. Similarly, the sensitivity recorded for models of three species was low in Bohle Western Upstream arm and Dungeness Creek recorded high percentages of false positives for four species. Testing of the ecological model has thus rapidly identified that something within these estuaries needs to be investigated and that focusing research efforts on these estuaries could provide the answer to what that is. In conclusion, although at this stage it is not possible to determine the reasons underlying poor predictions of individual species models, the research prioritization allows for focused research efforts. This will eventually lead to increased understanding of the ecology and the potential impacts of anthropogenic activities on intertidal crab spatial distribution patterns and ultimately feeds back to improved models.

# **Chapter 7: Differences in resource use patterns create functional differences across spatially distinct intertidal crab assemblages**

## **7.1 Introduction**

Tropical estuaries comprise a diverse habitat landscape in which the provision of key ecosystem processes relies on the spatial distribution and biological interactions of the faunal assemblages mediating these processes (Sheaves, 2005, Barbier et al., 2011). Consequently, shifts in faunal assemblages across landscapes can disrupt the functioning of ecosystems, especially when the degree of functional redundancy between assemblages is low (Schwartz et al., 2000, Mistri et al., 2001, Bellwood et al., 2003). Nonetheless, knowledge on the patterns of spatial distribution and ecological linkage of many faunal assemblages inhabiting tropical estuaries, in particular basal consumers, is restricted to small, within-habitat models that fail to incorporate the functional role of these assemblages within the broader context of the estuarine landscape (Nagelkerken et al., 2008, Barbier et al., 2011). Therefore, improved ecological models that integrate habitat associations and biological interactions of faunal assemblages within the estuarine landscape are critically needed to gain improved understanding of key ecosystem processes and potential changes to them.

Intertidal crabs are a dominant faunal component of tropical estuaries that is intimately linked to many fundamental ecosystem processes and to other estuarine organisms through trophic interactions and ecosystem engineering (Apel and Tuerkay, 1999, Kristensen, 2008, Amaral et al., 2009). While the diversity and the intricacies of many of their ecosystem interactions are still unclear (Kristensen, 2008), their trophic interactions provide a direct and identifiable link with the estuarine ecosystem. In fact, intertidal crabs occupy a pivotal position between primary production and detritus, and organisms at higher trophic levels, such as birds, aquatic crabs and fish (Sheaves and Molony, 2000, Bouillon et al., 2002). Additionally, because they reach high abundances in many habitats

(Kristensen, 2008, Nagelkerken et al., 2008), intertidal crabs have a substantial impact on the energy flow through tropical estuaries (Koch and Wolff, 2002, Nordhaus, 2004).

A broadly applicable ecological model of habitat associations of intertidal crabs occupying the low intertidal zone was developed in Chapter 6. This model shows that intertidal crabs have stable, predictable habitat associations. In particular, banks with high structural complexity, provided by plants and fallen timber, and rock walls were dominated by the genus *Metopograpsus*, banks with low structural complexity by the genus *Uca*, and mudflats by *M. japonicus*. These habitats are prevalent across estuaries in North Queensland, Australia. This ecological model of habitat associations provides valuable information regarding shifts in the taxonomic composition of species assemblages across habitats (Fausch et al., 2002). However, the consequences of these taxonomic shifts for energy transfer through tropical estuaries are still undefined because patterns of resource utilization have not been integrated into habitat association models.

Diet studies on intertidal crabs are generally conducted at site-specific scales (Kanaya et al., 2008, Mazumder and Saintilan, 2010, Kristensen et al., 2010). Consequently, extrapolation of results from these studies into resource use patterns within the estuarine landscape is limited because of unknown variability in sources of nutrition across habitats. Additionally, in most studies, diet items and sources of nutrition are coarsely defined due to methodological constraints. For instance, the resolution of gut content data is limited because crabs use a gastric mill to grind up food items. Similarly, analysis of stable isotope composition, which is based on the differential isotopic composition of carbon from different primary producers and of nitrogen across trophic orders, becomes difficult to interpret when many potential food sources are available (Bouillon et al., 2008). This is particularly problematic in estuarine sediments where many of the available food items have similar isotopic signatures (Bouillon et al., 2008). Additionally,  $\delta^{13}\text{C}$  values can only provide information on potential diets based on signatures of primary producers that were entered into the analysis (Abrantes and Sheaves, 2008, Bouillon et al., 2008). Finally, analyses of fatty acids, which have the ability to provide more fine detailed information regarding resource use, depend on an involved chemical process which is often financially prohibitive (but see Meziane et al., 2006, Takagi et al., 2010).

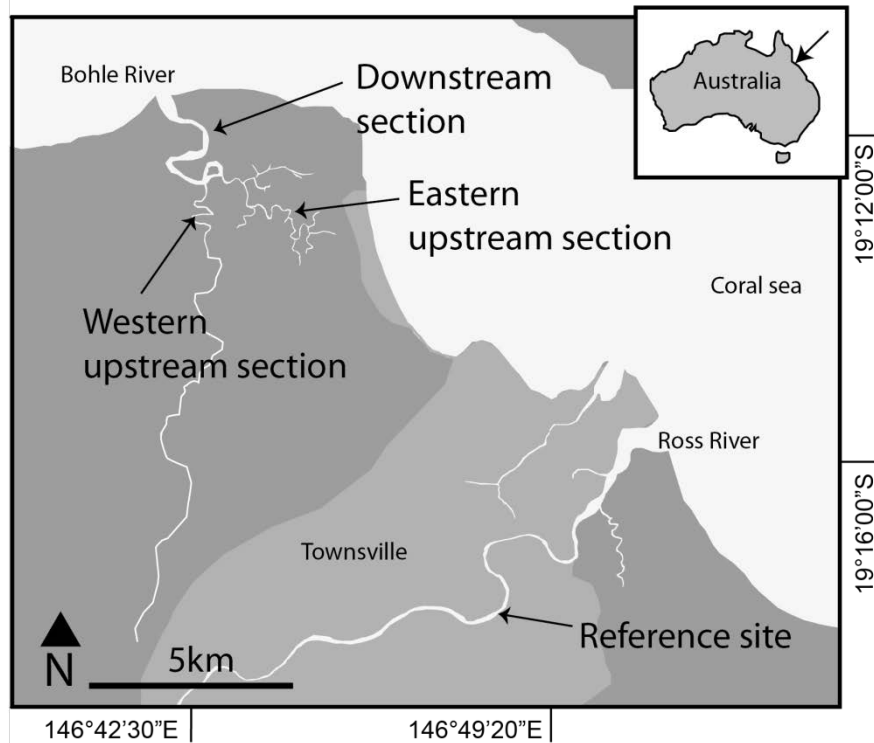
Despite the inability of stable isotope analysis to provide highly detailed information regarding the exact composition of intertidal crab diets, this method can provide valuable insights into trophic niche use (Ikeda et al., 2010, Saintilan and Mazumder, 2010, Turner et al., 2010). Different isotopic signatures have been found for distinct crab assemblages and even for the same species across habitats along intertidal transects, indicating that crabs can be involved in different trophic interactions across different habitats (Kon et al., 2007, Saintilan and Mazumder, 2010). However, shifts in primary producers across habitats also occur making interpretations of isotopic shifts between consumers across habitats difficult (Bouillon et al., 2008). Nonetheless, in well mixed estuaries, shifts in primary producers at small scales (meters to one kilometer) are unlikely to occur (Kon et al., 2007, Saintilan and Mazumder, 2010). Consequently, analysis of stable isotope compositions of intertidal crabs across closely located sites can provide the necessary knowledge regarding differences in resource use by distinct taxonomic assemblages within the habitat landscape.

Knowledge of diets and sources of nutrition are necessary to underpin understanding of functional variation and connectivity across habitat landscapes. In this chapter I investigate the dietary resource use patterns of intertidal crabs using stable isotope analysis, and integrate that understanding with the habitat association model developed in Chapter 6.

## **7.2 Methods**

Sampling was conducted in Bohle River estuary (19°12'00"S, 146°42'30"E, Fig. 7.1). Three main sections (downstream section, Eastern upstream section and Western upstream section) were delineated in the estuary (Fig 7.1) and samples of crabs collected at one location in each section. The location in the downstream section was sampled on 6 October 2010; the location in the Eastern upstream section, which is situated in a national park, was sampled on 23 September 2010; and the location in the Western upstream section was sampled on 9 September 2010. The latter location was approximately 15km, measured along the river, downstream from a sewage treatment plant which continuously expelled organically enriched freshwater. Little other freshwater inflow occurred during the

sampling period which corresponded with the end of the dry season. Sampling was conducted during ebb of daytime spring tides.



**Figure 7.1** Location of study system (Bohle River) with different sections, and location of the reference site for isotopic signatures of primary producers (Ross River)

The extent of each sampling location was small (1km) so regular tidal movements are likely to have homogenized the organic matter pool available in sediments on the intertidal banks of each site. Consequently, shifts in algal stable isotope signatures between habitats within locations are unlikely (Bouillon et al., 2008) and stable isotope samples of the crabs can be compared directly for differences in resource use. Within each location, *U. coarctata* and *U. seismella* were sampled together on flat intertidal banks bordered by *Avicennia marina*. *Metapograpsus frontalis* were caught on intertidal banks of medium to high structural complexity bordered by *Cerriops* spp.. Finally, *M. latifrons* were collected from high structure intertidal banks, bordered by *Rhizophora stylosa* at the downstream and Western upstream sections, and from fallen logs in the Eastern upstream section



where *R. stylosa* vegetation was absent. At each location, three individuals per species were caught by hand, euthanized in ice-water slurry and frozen until analysis.

White muscle tissue from legs and claws of crabs was removed (Yokoyama et al., 2005), dried to constant weight at 60°C and homogenized with a mortar and pestle into a fine powder (Abrantes and Sheaves, 2009). Samples from each individual crab were then weighed to 0.01mg and analyzed at the UC Davis Stable Isotope Facility (USA) using an elemental analyzer interfaced with an isotope ratio mass spectrometer. Results were expressed as deviations relative to the international standards for carbon and nitrogen. Carbon was of main interest in this study. However, nitrogen was included to allow investigation of any differences in trophic levels between crabs and the potential organic matter pollution across the estuary (Bouillon et al., 2008). Data were plotted to explore relationships between them and differences between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of *Metopograpsus* spp. and *Uca* spp. were analyzed with a one way-ANOVA, using family as factor.

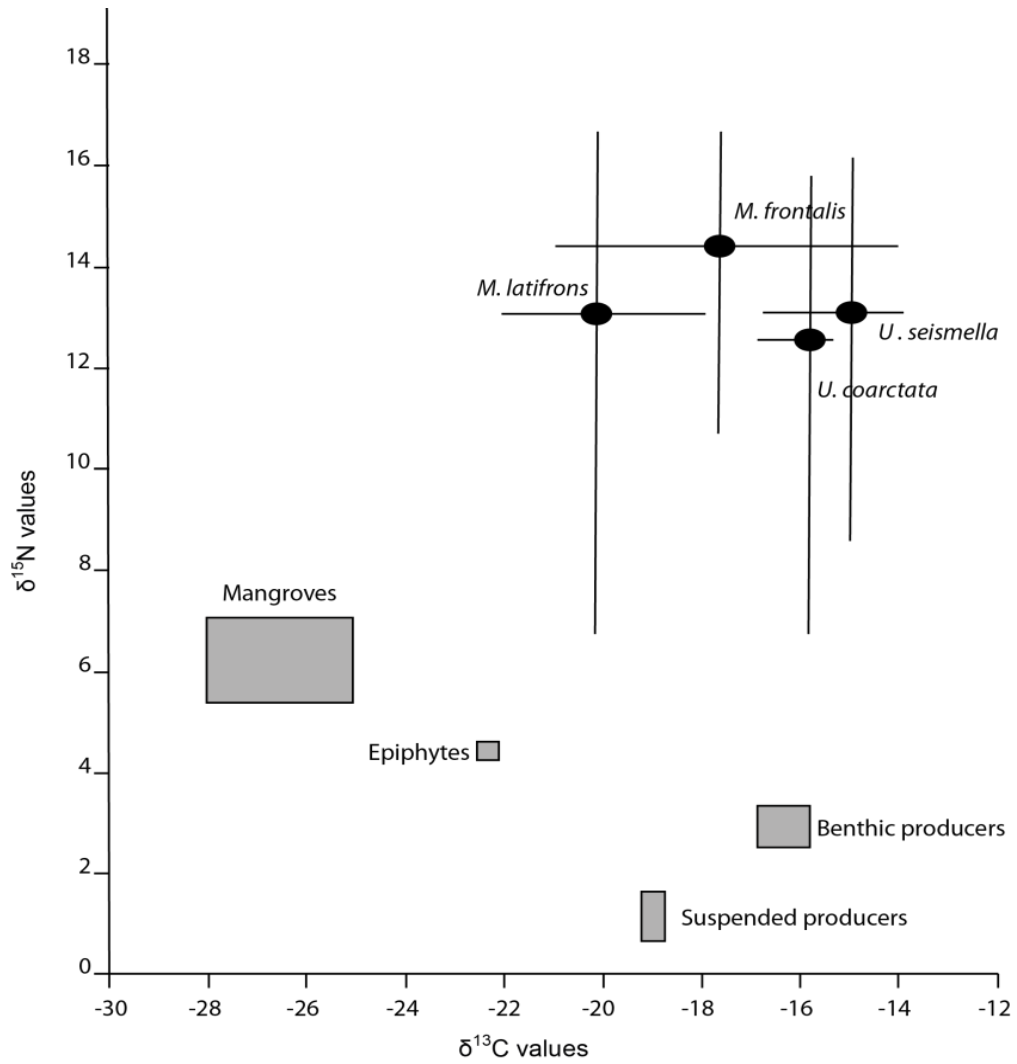
To relate values of crabs to sources of nutrition, previously reported  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of primary producers from Ross River (Abrantes and Sheaves, 2008) were included for analysis. These values included: microphytobenthos (collected from obvious mats on the sediment surface), epiphytes (removed from mangrove roots) comprising filamentous green and red algae and diatoms, suspended producers (collected with 250 and 53 $\mu\text{m}$  plankton nets) which included living plankton and suspended particulate organic matter and finally, fresh and decomposing mangrove leaves (Abrantes and Sheaves, 2008, Fig. 7.2).

### 7.3 Results

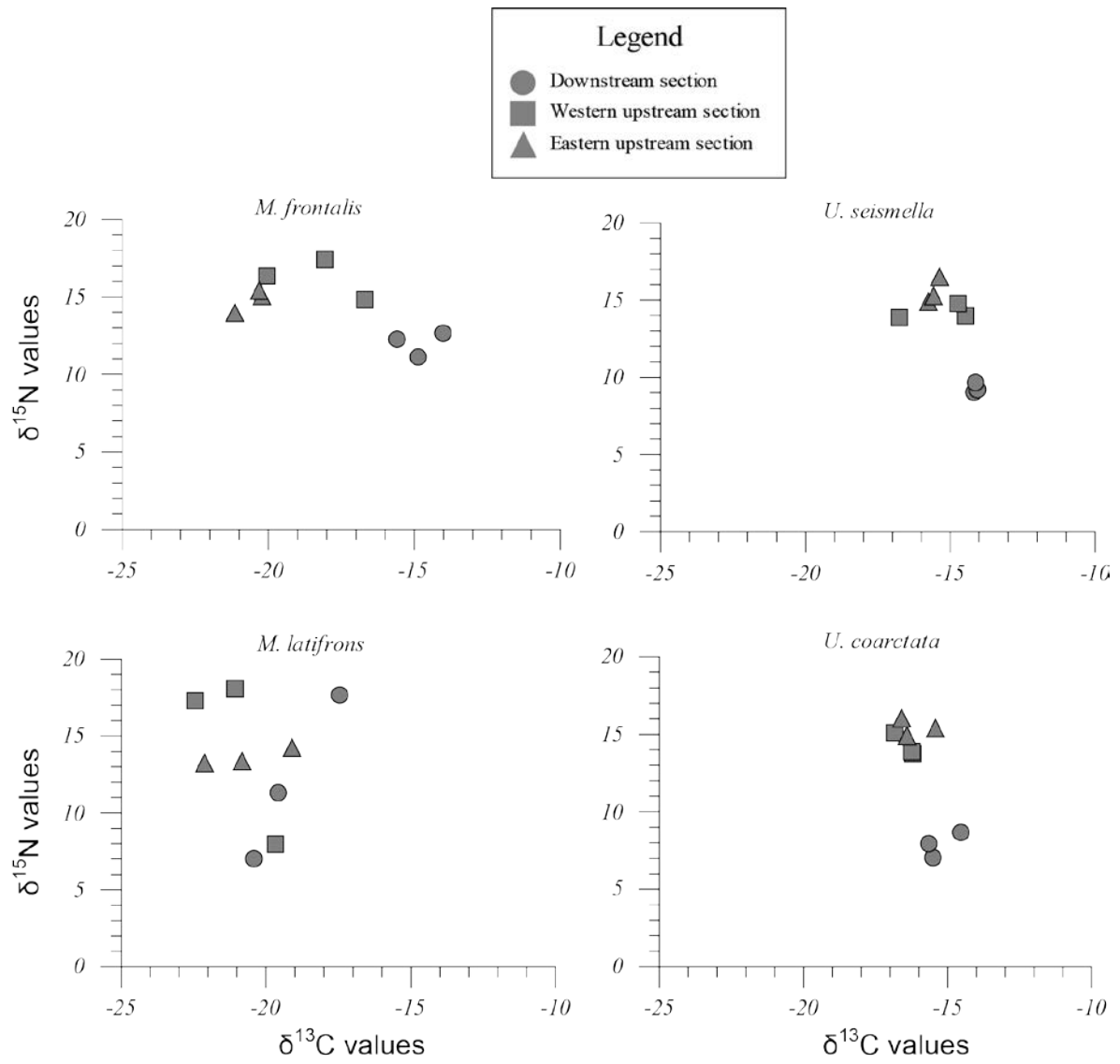
$\delta^{13}\text{C}$  values of *Uca* spp. aligned closely with isotopic signatures previously reported for microphytobenthos producers in Ross River (Abrantes and Sheaves, 2008, Fig. 7.2). By contrast, the more depleted  $\delta^{13}\text{C}$  values of *Metopograpsus* spp. relative to *Uca* spp. (ANOVA:  $F=33.98$ ,  $df =34$ ,  $p=0$ ) indicate that *Metopograpsus* are influenced by a more depleted source than *Uca* spp. (Fig. 7.2). The  $\delta^{13}\text{C}$  of the *Uca* spp. were well separated

from those of *M. latifrons*, but overlapped partially with those of *M. frontalis* (Fig. 7.2). There was little obvious variability in  $\delta^{13}\text{C}$  values between locations, except for *M. frontalis* (Fig. 7.3). Much of the variation appears to relate to the biological characteristics of the crabs; all  $\delta^{13}\text{C}$  values of *M. frontalis* below -17 were from molting individuals and all of those, except the most depleted one, were males.

$\delta^{15}\text{N}$  values were 1 to 3 trophic levels above primary producers (Bouillon et al., 2008), but no consistent difference was found between *Metopograpsus* spp. and *Uca* spp. (ANOVA:  $F=1.04$ ,  $df=34$ ,  $p=0.32$ ) (Fig. 7.2).  $\delta^{15}\text{N}$  values were highly variable, which for both *Uca* spp. could be explained by a difference between upstream and downstream locations (Fig. 7.3). Similarly,  $\delta^{15}\text{N}$  values of *M. frontalis* were slightly lower in the downstream than the upstream locations (Fig. 7.3).  $\delta^{15}\text{N}$  values of *M. latifrons* did not show an obvious pattern (Fig. 7.3).



**Figure 7.2** Mean and minimum and maximum range of isotopic values recorded for intertidal crabs species in Bohle River estuary, and minimum and maximum range isotopic values (grey boxes) of primary producers in the Ross River estuary (modified from Abrantes and Sheaves, 2008)



**Figure 7.3**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values recorded for individuals of four crab species across locations in three sections of the Bohle River estuary (each sample comprises three individual crabs)

## 7.4 Discussion

*Metopograpsus* spp. and *Uca* spp. display unique resource use patterns.  $\delta^{13}\text{C}$  values of *Uca* spp. were comparable to signatures of microphytobenthos collected in mangrove wetland pools in nearby Ross River (Fig. 7.2, Abrantes and Sheaves, 2008). By contrast,  $\delta^{13}\text{C}$  values of *Metopograpsus* spp. were generally more depleted and more variable than those of *Uca* spp. and fell in between signatures of microphytobenthos, epiphytes and suspended producers reported in Ross River (Fig. 7.2, Abrantes and Sheaves, 2008). Although Bohle River and Ross River are only approximately 15km apart (Fig. 7.1), signatures obtained for primary producers in one system might not be directly transferable to the other (Bouillon et al., 2008). Nonetheless, the results match with the general assumption that *Metopograpsus* spp. are opportunistic feeders that gain a large part of their nutrition from epiphytic algae (Dahdouh-Guebas et al., 1999, Poon et al., 2010, Nordhaus et al., 2011) while *Uca* spp. are sediment deposit feeders, which likely derive the bulk of their nutrition from microphytobenthos (Hsieh et al., 2002, Kanaya et al., 2008, Nagelkerken et al., 2008).

The habitat associations and feeding mechanisms of *Uca* spp. and *Metopograpsus* spp. further support the idea of trophic niche segregation between the two genera. *Uca* spp. generally have restricted home ranges and therefore need to obtain food in close proximity to their burrows (Zeil, 1998, Zeil and Hemmi, 2006). Additionally, given that they are associated with areas of low structural complexity (Chapter 6), it is unlikely that they would be feeding on epiphytic algae, because the latter need structure to grow on. Furthermore, *Uca* spp. possess an intricate sediment feeding mechanism which involves the accumulation of sediment balls in the buccal region, from which food items are sorted using specifically designed setae on their mouthparts (Icely and Jones, 1978, Arruda Bezerra et al., 2006). By contrast, *Metopograpsus* spp. have a morphology more suited for browsing and scraping algae (Shaw and Tibbetts, 2004). Consequently, microphytobenthos is unlikely to provide a large contribution to the diet of *Metopograpsus* spp.. In conclusion, the two families are likely to have low dietary overlap, and so participate in different trophic webs and to provide different trophic ecosystem services within the estuarine habitat landscape.

Fundamental differences in diet could have substantial implications if there is a change in the distribution and availability of different habitat types within the landscape. For example, with increasing urbanization and port developments, the construction of rock walls is likely to increase in tropical estuaries (Morley et al., 2012). The habitat association model previously developed for intertidal crabs occupying the low intertidal zone (Chapter 6) showed that rock walls are dominated by *Metopograpsus* spp. while structurally simple banks are dominated by *Uca* spp. Consequently, the differences in sources of nutrition used by the two taxa indicate that changes in species composition that flow on from changes in habitat type (Chapter 6) will result in even more fundamental changes because different crab assemblages occupy different trophic niches.

The concept that *Metopograpsus* spp. opportunistically supplement their diet with animal material (Poon et al., 2010, Nordhaus et al., 2011) is not strongly supported by the data.  $\delta^{13}\text{C}$  values of both *Metopograpsus* spp. were more variable than those recorded for *Uca* spp., suggesting potential opportunistic feeding, however, variability in  $\delta^{13}\text{C}$  values recorded for *M. frontalis* could be explained by changes in location. Additionally, since all  $\delta^{13}\text{C}$  values of *M. frontalis* below -17 were from molting individuals and all of those, except the most depleted one, were males, the variability might also be due to differences in sex or molting stage. Finally, if *Metopograpsus* spp. were feeding on animal material, they would be expected to occupy a noticeably higher trophic position than *Uca* spp. However,  $\delta^{15}\text{N}$  values did not support trophic level differences between the two taxa.

The patterns in  $\delta^{15}\text{N}$  values observed for three of the four species were mainly related to upstream versus downstream sections. Despite known sewage input in the Western arm of the Bohle River estuary, there is no real evidence of greater impact of sewage pollution from the data presented here, which would be expected to result in enriched  $\delta^{15}\text{N}$  values in the Western arm. However, the large difference between up- and downstream sections for both *Uca* spp. could reflect trapping of  $\delta^{15}\text{N}$  enriched water in the upper estuary as a whole. Whatever the situation, the spatial variation in  $\delta^{15}\text{N}$  values does support the notion that intertidal crabs have the potential to be suitable indicators of organic pollution (Penha-Lopes et al., 2009).

# **Chapter 8: Progressing from ecological knowledge to a management baseline with the aid of citizen scientists**

## **8.1 Introduction**

In the next few decades the trend of important urban and economic development around tropical estuaries is expected to continue and even intensify (Seto, 2011). These developments put huge anthropogenic pressure on estuaries (Alongi, 2002, Duke et al., 2007). Additionally, a large part of the population in these areas has restricted capacity to adapt to climate change, while being directly dependent on estuarine goods and services to a large extent (Seto, 2011). Consequently, there is a critical need for management that ensures future sustainable and equitable use of tropical estuaries (Duke et al., 2007, Martinuzzi et al., 2009). Such management needs to be founded on scientific baseline data capable of providing realistic predictions regarding the outcomes of urbanization and climate change for the functioning of estuaries and the goods and services they provide. The spatial extent of such ecological baselines should be large enough to include the system-wide scale at which the effects of urbanization and climate change are likely to be seen (Fausch et al., 2002). Additionally, to remain ecological relevant, baselines should include the habitat-scale at which faunal patterns are structured (Fausch et al., 2002). Finally, the baseline understanding needs to be applicable across estuaries to allow for easy transfer of management strategies (Sheaves and Johnston, 2010).

The ecological understanding gained in this thesis regarding habitat associations of intertidal crabs within and among estuarine landscapes and the methodology developed to collect spatial data at these scales, provides a powerful framework for the collection of ecological baseline data. Firstly, the conceptual model of intertidal crab habitat associations provides an ecologically meaningful division of the low intertidal zone and thus allows for the design of scientifically founded baseline studies. Secondly, the photographic sampling method used to develop the ecological model of habitat associations provides an easy to use, low cost sampling protocol capable of collecting specific baseline data necessary to underpin management and monitoring applications

across large landscape level scales (Fausch et al., 2002, Chapter 3). Thirdly, the strong ecological linkage (Angsupanich and Aksornkoae, 1996, Apel and Tuerkay, 1999, Amaral et al., 2009), short life spans (Nobbs and McGuinness, 1999, Hilty and Merenlender, 2000) and restricted home ranges (Cannicci et al., 1996a, Layne et al., 2003, Zeil and Hemmi, 2006, Dauvin et al., 2010) of intertidal crabs mean that monitoring and management applications developed based on habitat associations of intertidal crabs can provide for rapid, local detection of changes that reflect system wide impacts on estuarine structure and function. Finally, the potential of intertidal crabs as biological indicators has already been demonstrated by changes in a diverse range of attributes in response to altered estuarine conditions, including: behavior (Bartolini et al., 2009), biomass, diversity (Cannicci et al., 2009) and reproductive success (Penha-Lopes et al., 2009). Anthropogenic activities are thus affecting intertidal crab populations, so when this results in distributional changes, ecological baseline data regarding spatial distribution patterns could be a highly valuable tool for management of tropical estuaries.

The collection of baseline data at these large landscape levels requires a large investment of resources, particularly personnel to collect and analyze these data. For example, baselines of comparable intertidal invertebrate groups, such as beetles and spiders, in temperate estuaries are supported by large, broad scale datasets, collected over decades of research (Desender et al., 2010). As a result, baselines build using these datasets have strong prediction and detection powers because they allow for clear definition of the habitat associations of these invertebrates (Desender et al., 2010), their bio-indicator capabilities (Finch et al., 2007, Irmiler et al., 2002, Neto et al., 2010) and their ecosystem linkage (Ikeda et al., 2010). One way of achieving similar long term, broad scale datasets to support management baselines build using habitat-associations of intertidal crabs is via the involvement of citizen scientists.

Citizen scientists are people that voluntary engage in science, but who not necessary have a scientific background (Miller-Rushing et al., 2012). Additionally, in contrast to volunteers, citizen scientists generally operate more independently and collect and/or analyze data often without direct supervision (Newman et al., 2012). Because of this more independent relationship between citizen scientists and researchers data can be gathered from a wider geographic range with higher temporal replication than when researchers



have to be present (Dickinson et al., 2012). Citizen scientist can thus provide the necessary long term, broad scale datasets. Additionally, involvement of citizen scientists increases intellectual capital regarding environmental issues and improves interactions between ecological management and the social and economic context of the people it will affect (Cooper et al., 2007, Conrad and Hilchey, 2011). The resulting wider socio-economic debate concerning ecosystem management ultimately leads to the development of holistic approaches that incorporate both sustainability and equitability principles (Glaser, 2003). Despite the many benefits and the large number of citizen science projects developed across ecosystems, little scientific literature is published using the citizen science data (Galloway et al., 2006, Conrad and Hilchey, 2011). This is principally because of concerns about the accuracy of data collection and analysis (Galloway et al., 2006, Frost Nerbonne, 2008, Delaney et al., 2008, Silvertown, 2009, Conrad and Hilchey, 2011). Therefore, the aim of this chapter is to determine the robustness of the photographic protocols developed in Chapter 3 for use by citizen scientists to collect accurate data to support scientific baselines for use in estuarine management.

## **8.2 Accuracy of data collection and analysis**

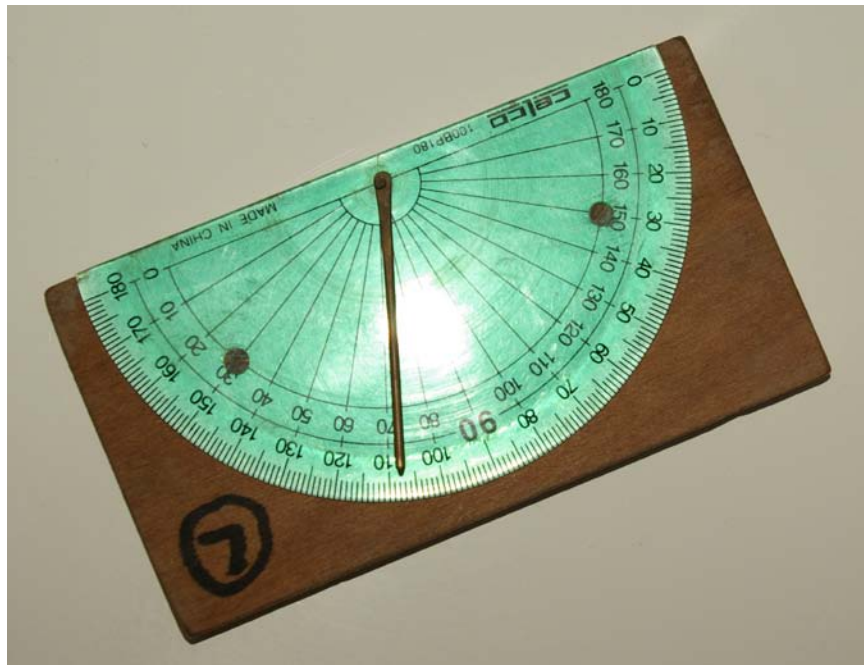
The quality of data-collection regarding the habitat-associations of intertidal crabs occupying the low intertidal zone using photography and citizen scientists is high because of the simple manipulations involved. In fact, most variables relating to collecting data with photography can be measured independently, such as speed of the boat or distance from the crabs, or set beforehand, such as camera settings. Additionally, during this study high quality photographs of intertidal crabs were always collected by volunteers, with little prior training. Infrequently, the volunteer lost count of the number of photographs per site. However, volunteers were asked to start counting from zero if they lost count, thereby ensuring there were always enough photographs available for analysis. A minimal number of photographs were affected by visibility issues, mostly high contrast or blurring, making subsequent analysis difficult or impossible (see electronic appendix for examples of affected and suitable photographs). For example, a total of 2336 photographs were collected during the April 2011 and July 2011 Stuart Creek sampling trips. Only, 1% of these photographs were affected by high contrast, which made them generally unusable

and 7% were blurry. However, the bulk (70%) of the blurry photographs was still usable for identifying crabs. The researcher was present while the volunteers took the photographs. Hence, quality of photographs should be tested without the researcher being present if this technique is being used by independent citizen scientists. Nonetheless, photographic data are likely to be collected at a high standard by citizen scientists.

Photo-quadrats can be accurately analyzed for intertidal crab fauna, despite the higher level of skills needed. A high correlation was found for presence-absence, relative abundance and absolute abundance data analyzed repeatedly by an experienced observer or independently by experienced and inexperienced observers (Chapter 3). A repetition of this assessment with more volunteers and including data regarding age, education and prior volunteering experience would allow for the development of appropriate training and the coupling of expertise levels with analysis of different data-types, thereby augmenting data accuracy (Galloway et al., 2006, Delaney et al., 2008). Additionally, photographic data can always be checked either by a researcher or by other volunteers because the photographs provide a permanent record (Basset et al., 2000). Finally, when broader spatial and temporal datasets regarding habitat associations of intertidal crabs become available, outliers within these datasets, due to inaccurate analysis of photographs, are easier to detect. Hence, the involvement of many citizen scientists eventually provides a safety net against data-inaccuracy.

Accuracy of data collection on the physical environment can be ensured by training volunteers and by periodically checking of data by researchers. The physical factors measured in a citizen science project can range from simple to complicated depending on the aim and study design. Consequently, projects should be classified based on technical difficulty and matched with training to guarantee data accuracy (Delaney et al., 2008). However, many of the physical variables used to identify the habitats of individual species in this study were easy to measure and could be deduced from photographs making it easy to check them by a researcher at any time. For instance, structural variables such as the amount of logs and various types of roots were deduced, in terms of the percentage of the photo-quadrat they occupied, from the same photographs used to identify intertidal crabs. Similarly, an overview photograph of the site could be taken to allow general variables such as vegetation type, presence or absence of canopy overhang and broad

classes of substratum to be established. Finally, bank angle is one crucial factor that will need to be measured in every project because it is needed to standardize photographs (Chapter 3). However, bank angle can be measured with a simple inclinometer (Fig. 8.1). This is an easy to use tool that is simply held parallel to the surface of the bank and allows the angle of the bank relative to the horizon to be read.



**Figure 8.1** An easy to use inclinometer to measure bank angles

### 8.3 Conclusion

From a scientific standpoint, there should be little impediment to using citizen scientists in the collection of baseline data for monitoring and management projects using the photographic method. At each step in the data collection and analysis process measurements can be put in place to ensure accuracy of data collected by citizen scientists. Additionally, the permanent record of samples collected using photography means that at each stage data can be checked. Hence, citizen scientists have the capacity to rapidly provide the broad-scale data necessary to underpin landscape level baselines for management and monitoring. This would substantially improve current management

practices which often lack a sound scientific baseline (Cox et al., 2005, Moss et al., 2005, Sheaves and Johnston, 2010). Furthermore, the involvement of citizen scientists has the added advantage of greater transparency of science and management and wider debate of the findings and actions they develop in a social and economic context (Cooper et al., 2007, Conrad and Hilchey, 2011). Given that many tropical estuaries are in areas where social and economic development are skyrocketing (Seto, 2011), such improved transparency and debate, via the involvement of citizen scientists, will profit the future sustainable and equitable use of estuarine goods and services.

# **Chapter 9: A new landscape level understanding regarding the structure and functioning of intertidal crabs in tropical estuaries**

## **9.1 Introduction**

This thesis provides an extensive landscape level understanding of the spatial organization of intertidal crab assemblages within the low intertidal zone of tropical estuaries, and develops an ecological model of the habitat associations of these crabs. This ecological model demonstrated strong, predictable crab/habitat associations within and among estuaries, and revealed the low intertidal zone as a heterogeneous habitat landscape in which crab assemblages form distinct taxonomic communities (Chapter 5 and 6). By developing spatial knowledge at a large landscape scale while maintaining definition regarding the habitat matrix that comprises this landscape, the ecological model has the potential to provide a context within which to integrate the results of previous local scale studies (Chapter 5). Additionally, the study established the high stability, predictability and transferability of spatial distribution patterns within and across tropical estuaries (Chapter 6). Thus, this thesis provides a fresh perspective to previous studies that were predominantly focused at the local scale, and establishes the broad spatial understanding needed as a basis for the integration of this key faunal group in models of ecosystem processes operating within and across tropical estuaries. In the final chapter, I aim to deepen the understanding gained in this thesis regarding spatial distribution patterns of intertidal crabs across the estuarine habitat landscape. Therefore, I discuss the potential mechanisms underlying the observed spatial distribution patterns and expand on their implications for the ecological function of intertidal crabs in the estuarine ecosystem.

## 9.2 Mechanisms underlying spatial distribution patterns within and across estuaries

The ecological model allows evaluation of the relative importance of niche-assembly versus dispersal-assembly mechanisms, two contrasting and highly debated mechanisms in governing spatial distribution patterns of organisms (Whitfield, 2002), in the context of intertidal crabs within tropical estuarine landscapes. Niche-assembly theory posits that the spatial organization of communities is determined by interactions with the biotic and abiotic environment (Tilman, 1982, Potts 2004). By contrast, dispersal-assembly theory postulates that the spatial organization of communities is governed by dispersal, chance and history (Hubbell, 1997, Gilbert 2008). The existence of highly predictable crab/habitat associations within and among tropical estuaries (Chapter 5 and 6) agrees with previous evidence of associations with environmental factors at small scales (Koch et al., 2005, Arruda Bezerra et al., 2006, Takeda, 2010, Chapter 1). The within estuary scale pattern of habitat-association further agrees with strong associations with the physical environment at the 1m to 1km scale observed for other estuarine faunal communities, such as sessile root epibionts (Fransworth and Ellison, 1996). By contrast, the high predictability of habitat associations among estuaries contradicts observations of large variability in species composition of root epibionts among mangrove cays (Fransworth and Ellison, 1996) and fish fauna among estuaries (Sheaves and Johnston, 2009). Nonetheless, it confirms a strong influence of the environment of the spatial distribution of intertidal crabs. This matches with the different morphological, behavioral and physiological adaptations of intertidal crabs (Chapter 1) which allow for a diversity of competitive strategies within a heterogeneous landscape, such as that of tropical estuaries (Lee 2008). The effect of the latter adaptations is expressed in the existence of distinct taxon-specific communities (Chapter 5 and 6) and in the breadth of the habitat associations of the species investigated. For example, *U. coarctata* occurred in a wide range of sites and is thus more generalist in its association with environmental gradients structuring intertidal crab assemblages than for instance *U. seismella* or *M. latifrons* (Chapter 5 and 6). The combined evidence of strong relationships with the environment suggests that spatial distribution patterns of intertidal crabs both within and among tropical estuaries are

primarily driven by spatial niche associations, rather than mechanisms that are neutral to the environmental landscape (Gilbert, 2008, Chapter 5).

Local factors are more likely to drive spatial niche structure than large along-estuary gradients. The main along-estuary gradient that has often been suggested to influence the spatial distribution of intertidal crabs is the salinity gradient (Ewa-Oboho, 1993, Ashton et al., 2003, Koch et al., 2005, Ravichandran et al., 2007). In fact, Ness (1972) identified an upstream gradient in species composition in Ross River estuary and attributed this to salinity changes. Only the downstream section of Ross River was studied in this thesis (Chapter 6). Nonetheless, no systematic differences were detected in the predictive abilities of the models in upstream versus downstream components in the other estuaries investigated (Chapter 6). This is not necessarily surprising because spatial distribution patterns do not always match with osmoregulation capacities and salinity tolerances (Frusher et al. 1994). For example, a relationship between salinity and spatial distribution can be weakened because crab physiology can acclimatize to local temperature and salinity conditions and osmotic stress can be lowered via mechanisms such as movements of the abdomen, increased cleaning behavior, or the use of microhabitat features such as burrows and shelters (Holliday, 1985, Greenaway et al., 1996, McGaw, 1999, 2001). Furthermore, the cost of osmoregulation is often traded off against other costs. For instance, the salinity preference range of *Hemigrapsus nudus* is lowered by 12‰ when shelter, in the form of boulders, is present (McGaw, 2001). In conclusion, within the estuarine range considered in this thesis, salinity only has a weak influence on intertidal crab spatial distribution patterns. Hence, changes in species composition along estuaries reflect changes in habitat availability more than large gradients in salinity.

The high heterogeneity of habitats available within the low intertidal zone (Lee, 2008, Chapter 5 and 6) combined with the restricted home range of intertidal crabs (Cannicci et al., 1996a, Zeil and Hemmi, 2006) implies that the unique adaptations of different species of intertidal crabs to local conditions, such as sediment grain size, organic matter content, water content, microclimate, structural complexity and food availability (Chapter 1), are likely to have a strong influence on their spatial distribution patterns. The main adaptations in which intertidal crabs occupying the low intertidal zone differ (Chapter 1) can be grouped in three categories: firstly, adaptations to protect against the environment

(including the physical environment and predators) via the ability to construct shelters, secondly, adaptations to communicate and thirdly, adaptations to obtain nutrition. All of these adaptations could have created the broad split between associations of Ocypodidae and Macrophthalmidae communities versus Grapsidae communities for habitats with different levels of structural complexity observed in the spatial distribution model (Chapter 6). Nonetheless, the identity and relative importance of the different adaptations is likely to be species specific. For instance, for *U. seismella*, which has highly developed waving displays (von Hagen, 1993) which are restricted in areas with high structural complexity, the communication adaptations should have a strong influence on spatial distribution. Meanwhile, the ability of *U. seismella* to construct burrows (Eshky et al., 1995) means that their spatial distribution is likely only dependent on natural shelter availability to a limited extent. By contrast, for *M. latifrons*, which is a tree dwelling species (Sivasothi, 2000), the availability of natural shelter should be a strong influence in determining spatial distribution patterns. Similarly, because of the different adaptations to obtain nutrition, the distribution of macro-algae should be a major influence on the spatial distribution of *Metopograpsus* spp. (Poon et al., 2010, Nordhaus et al., 2011) while sediment food sources are likely to be more influential in governing Ocypodidae and Macrophthalmidae niche associations (Meziane et al., 2002, Hsieh et al., 2002). In conclusion, a diversity of abiotic conditions and food sources are critical to maintain niche structure of intertidal crabs.

The role of local predation or competitive interactions in modifying spatial niche patterns is unclear because evidence of these interactions is generally lacking. A wide diversity of organisms, ranging from aquatic fish, crabs and shrimp (Kneib and Weeks, 1990, Cannicci et al., 1996a, Sheaves and Molony, 2000, Behum et al., 2005, George et al., 2010) to terrestrial birds (Botto et al., 2000), mammals and reptiles (Teal, 1958) and to other intertidal crabs (McIvor and Smith, 1995, Takeda, 2010) prey on intertidal crabs. Differences in predation preferences for specific species have not been demonstrated. However, differences in predation rate between sexes of individual *Uca* spp. have been identified (Ribero 2003, Bergery 2008). This suggests the possibility that predators could also differentiate between species. Similarly, there is no evidence that intertidal crab species differ in nutritional value. Nonetheless, different taxonomic groups differ in their resource use (Chapter 7) and thus to represent different trophic pathways. Again, this suggests the possibility for the existence of predator preferences for specific species of



intertidal crabs. Competition mediated co-existence (Morris, 1996) could structure the overlapping spatial distributions of the spatial specialist *U. seismella* and the spatial generalist *U. coarctata* because of broader habitat preferences of the latter. Additionally, low levels of competition have been identified for some intertidal crabs. For example, *Neohelice granulata* and *Cyrtograpsus angulatus*, two species common in salt marshes along the South-West Atlantic coast, rarely co-exist in the same habitat (Martinetto et. al., 2011). However, when they do, *N. granulata* can restrict the distribution of *C. angulatus* (Martinetto et. al., 2011). Such evidence of direct competition, however, is scarce. The absence of evidence for both competition and predation makes it hard to draw conclusions about the role of these biotic interactions in governing spatial distribution patterns. Nonetheless, recent insights in the potential of intertidal crabs to affect the structure and functioning of the estuarine ecosystem via trophic interactions and ecosystem engineering underline the importance of biotic processes (Cannicci et al., 2008), thereby also indicating their potential in influencing spatial distribution patterns.

### **9.3 Implications of spatial distribution patterns within and across estuaries for the ecological role of intertidal crabs**

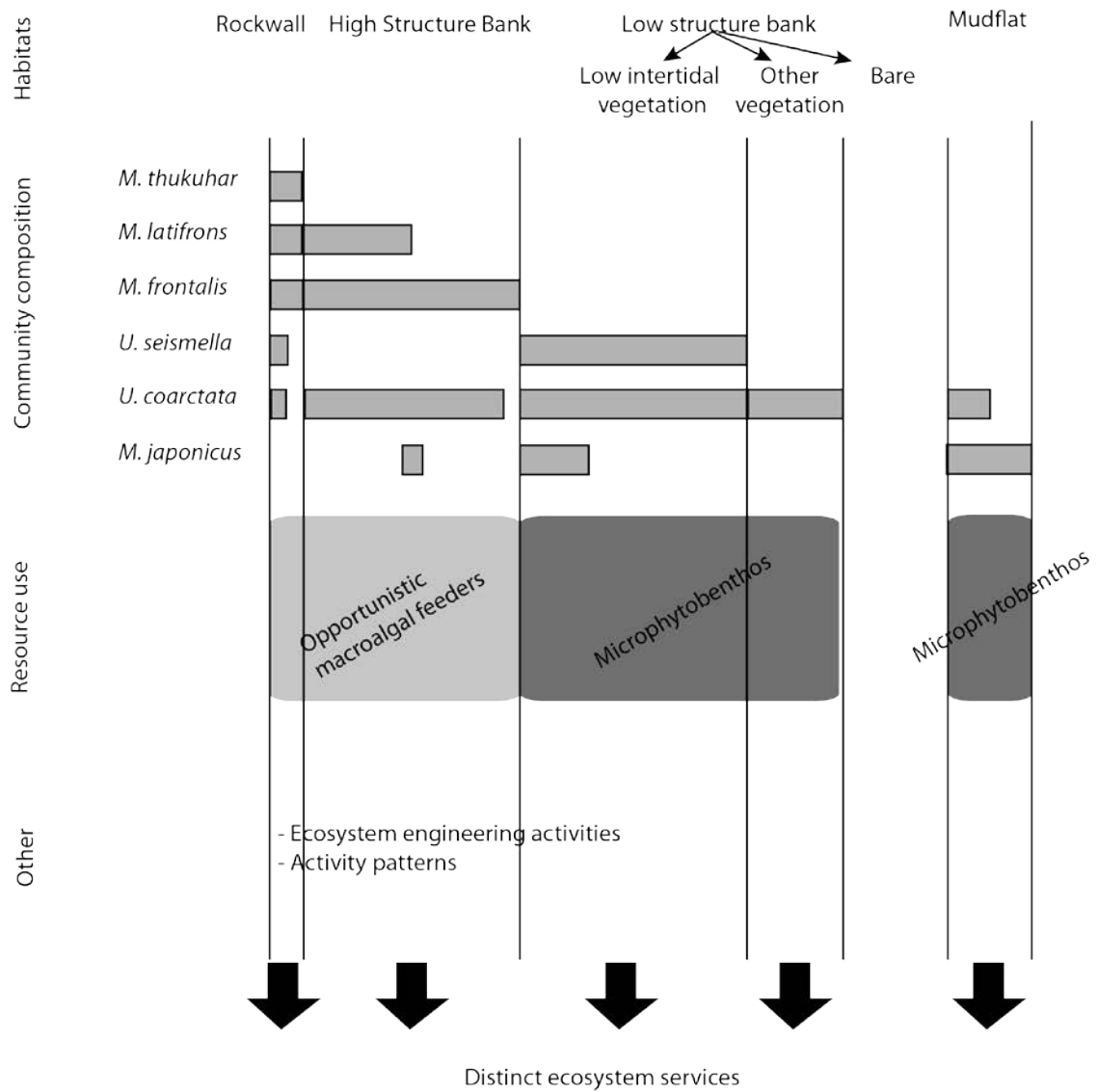
The model of habitat associations provides the statistical basis for an ecologically meaningful division of the low intertidal landscape because of the clear associations between crabs and identifiable habitats and between crabs and other estuarine components. In fact, distinct predictable associations were found between intertidal crab communities and habitats defined by simple morphological factors. Additionally, the taxonomic identity of these spatially distinct communities is consistent with specific adaptations of intertidal crab species (Chapter 1) and is mirrored in patterns of resource use (Chapter 7). Furthermore, the taxonomic communities provide different ecosystem engineering effects (Kristensen, 2008). For example, *Uca* spp. and *M. japonicus* communities create niches for other sediment organisms and influence bacterial productivity via changes in sediment chemical properties, as a result of their specific burrowing behavior and sediment feeding mechanisms (Kristensen, 2008), which are absent in representatives of the *Metopograpsus* spp. community (Chapter 1).

Because of the ecological linkages implied by the pattern of spatial distribution of intertidal crabs, the integration of this distribution pattern has the potential to form the basis for the development of detailed models of the ecological role of intertidal crabs in the estuarine ecosystem. For example, although a trophic flow model developed for *Uca* spp. within the Caeté estuary, Brasil (Wolff et al., 2000) gives an overall estimate of the ecosystem input of these crabs via their trophic interactions, it lacks definition at smaller habitat scales. Interactions at these smaller habitat scales are the ecological basis for the development of ecosystem models at landscape scales (Fausch et al., 2002). Consequently, the ability to precisely quantify the trophic role of intertidal crabs or to provide insights into how this role changes under different environmental conditions is restricted in Wolff et al. (2000) model. Because the ecological model of habitat associations developed in this thesis integrates fine scale habitat associations across a landscape scale, it provides a detailed spatial framework that could give context to studies like that of Wolff et al. (2000). Additionally, the ecological linkage of the pattern of spatial distribution of intertidal crabs implies that other ecological information layers such as activity patterns (Chapter 3), trophic interactions (Chapter 8) and ecosystem engineering (Kristensen, 2008) can be added (Fig. 9.1) to produce a more holistic model.

Recent harbor developments in Ross River (one of the model systems studied in Chapter 6) provide an example of the way in which different layers of ecological information can be integrated within the framework of the spatial model. The mouth of Ross River contains large expanses of mudflats inhabited by *M. japonicus*. However, the area of these mudflats has recently been halved due to reclamation to make way for a new marina bordered by rock-walls. The ecological model of habitat associations (Fig. 6.4 and Fig 9.1) shows that the faunal composition would shift from a *M. japonicus* community (mudflats) to a *Metopograpsus* spp. community (rock-walls). *Metopograpsus japonicus* is a sediment-deposit feeder, consuming mainly microphytobenthos (Kanaya et al., 2008, Kon et al., 2012) while *Metopograpsus* spp. are opportunistic macroalgal feeders, supplementing their diet with animal matter (Lee, 1998, Poon et al., 2010). Hence, in addition to a taxonomic shift, the layering of ecological information reveals that the change in land use is likely to result in the intertidal crabs at this location providing a different suite of ecosystem services. Due to differences in resource utilization patterns between *Metopograpsus* spp. and *Uca* spp. communities, similar shifts in function can also be

expected when shifts to *Uca* spp. habitat occur (Chapter 7). Additionally, intertidal representatives of Ocypodoidea and Grapsoidea have different life histories and therefore have different interactions with other components of the ecosystem (Kristensen, 2008), which will further affect the ecosystem services provided by intertidal crabs within different habitats. Given the rapid conversion of many estuarine habitats by human development, and the potential changes in habitat-landscapes as a result of climate change (Alongi, 2008), the model has the potential to lead to substantial advances in ecological understanding that can feed into an improved ability to make informed management decisions (Irmler et al., 2002).

Information layers



**Figure 9.1** Example of the process of information layering, using the ecological model of habitat associations as the framework

## 9.4 Remarks on the further development of the ecological model

The representatives of the taxonomic groups on which the ecological model is constructed are not the only intertidal crab species that inhabit the low intertidal zone. For instance, *Perisesarma longicristatum* (Sesarmidae) and *Australoplax tridentata* (Macrophthalmidae) were not sampled with photography but are well represented in hand catch samples of low intertidal banks of Stuart Creek (Chapter 3), and have been reported in the low intertidal of other estuaries throughout the Indo Pacific (Smith et al., 1991, Frusher et al., 1994, Meziane et al., 2006, Geist et al., 2011). Additionally, some habitats, such as sand flats, were not included in the ecological model of habitat associations because the model focused predominantly on areas with mud banks. Nonetheless, these habitats often have their own distinct fauna with their own characteristics. For example: *Mictyris longicarpus* (Micyrtidae) often dominates on sand flats (Takeda, 2010) and the few sites where *Uca vomeris* (Ocypodidae) was detected in this study were all characterized by sandy substratum. Because these species can contribute substantially to the intertidal crab fauna, their position in the ecological model of habitat associations deserves attention.

Many intertidal crabs have restricted home ranges (Cannicci et al., 1996a, Zeil and Hemmi, 2006). Consequently, a tree dwelling species, like *M. latifrons*, might remain in a single tree throughout its life. These small-scale structural elements are not differentiated when the structure is averaged over a site. This could explain the relative low sensitivity of the model of *M. latifrons* in some estuaries (Table 6.2). Such small habitat patches can be important for the survival of the species, for example as a refuge or a stepping stone (George et al., 2010). Hence, the importance of smaller within-site scale patterns cannot be neglected. Nonetheless, individual models of habitat-associations were successfully developed and tested for six species using simple morphological parameters. Overall, although gaps in our understanding of the spatial ecology of intertidal crabs remain, this study has provided advances in both our understanding and in the development of techniques that can provide robust models of intertidal crab spatial ecology at landscape scales.

## Bibliography

- ABRANTES, K. & SHEAVES, M. 2008. Incorporation of terrestrial wetland material into aquatic food webs in a tropical estuarine wetland. *Estuarine, Coastal and Shelf Science*, 80, 401-412.
- ABRANTES, K. & SHEAVES, M. 2009. Food web structure in a near-pristine mangrove area of the Australian Wet Tropics. *Estuarine, Coastal and Shelf Science*, 82, 597-607.
- ALONGI, D. M. 2002. Present state and future of the world's mangrove forests. *Environmental Conservation*, 29, 331-349.
- ALONGI, D. M. 2008. Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. *Estuarine, Coastal and Shelf Science*, 76, 1-13.
- AMARAL, V., PENHA-LOPES, G. & PAULA, J. 2009. Effects of vegetation and sewage load on mangrove crab condition using experimental mesocosms. *Estuarine, Coastal and Shelf Science*, 84, 300-304.
- ANGSUPANICH, S. & AKSORNKOAE, S. 1996. Macrobenthic fauna in shrimp-farms adjacent mangroves, Kradae Chae Canal, Ban Don Bay, southern Thailand. *Mer (Tokyo)*, 34, 75-81.
- APEL, M. & TUERKAY, M. 1999. Taxonomic composition, distribution and zoographic relationships of the Grapsid and Ocypodid crab fauna of intertidal soft bottoms in the Arabian Gulf. *Estuarine, Coastal and Shelf Science*, 49 suppl A, 131-142.
- ARAÚJO, M. B. & LUOTO, M. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, 16, 743-753.
- ARRUDA-BEZERRA, L. E. & MATTHEWS-CASCON, H. 2006. Population structure of the fiddler crab *Uca leptodactyla* Rathbun, 1898 (Brachyura: Ocypodidae) in a tropical mangrove of Northeast Brazil. *Thalassas*, 22, 65-74.
- ARRUDA BEZERRA, L. E., DIAS, C. B., SANTANA, G. X. & MATTHEWS-CASCON, H. 2006. Spatial distribution of fiddler crabs (genus *Uca*) in a tropical mangrove of northeast Brazil. *Scientia Marina*, 70, 759-766.

- ARRUDA BEZERRA, L. E. & MATTHEWS-CASCON, H. 2007. Population and reproductive biology of the fiddler crab *Uca thayeri* Rathbun, 1900 (Crustacea: Ocypodidae) in a tropical mangrove from Northeast Brazil. *Acta Oecologica*, 31, 251-258.
- ASHTON, E. C., MACINTOSH, D. J. & HOGARTH, P. J. 2003. A baseline study of the diversity and community ecology of crab and molluscan macrofauna in the Sematan mangrove forest, Sarawak, Malaysia. *Journal of Tropical Ecology*, 19, 127-142.
- AUSTIN, M. P. 1985. Continuum concept, ordination methods, and niche theory. *Annual Review of Ecological Systems*, 16, 39-61.
- BARBIER, E. B., HACKER, S. D., KENNEDY, C. J., KOCH, E. W., STIER, A. C. & SILLIMAN, B. R. 2011. The value of estuarine and coastal ecosystem services. *Ecological Monographs*, 81, 169-193.
- BARNES, R. S. K. 1967. The osmotic behaviour of a number of Grapsoid crabs with respect to their differential penetration of an estuarine system. *Journal of Experimental Biology*, 47, 535-551.
- BARTOLINI, F., CIMO, F., FUSI, M., DAHDOUH-GUEBAS, F., PENHA LOPES, G., CANNICCI, S. 2011 The effect of sewage discharge on the ecosystem engineering activities of two East African fiddler crab species: Consequences for mangrove ecosystem functioning. *Marine Environmental Research*, 71, 53-61.
- BARTOLINI, F., PENHA-LOPES, G., LIMBU, S., PAULA, J. & CANNICCI, S. 2009. Behavioural responses of the mangrove fiddler crab (*Uca annulipes* and *U. inversa*) to urban sewage loadings: Results of a mesocosm approach. *Marine Pollution Bulletin*, 58, 1860-1867.
- BAS, C., LUPPI, T. & SPIVAK, E. 2005. Population structure of the South American Estuarine crab, *Chasmagnathus granulatus* (Brachyura: Varunidae) near the southern limit of its geographical distribution: comparison with northern populations. *Hydrobiologia* 537, 217-228.
- BASSET, Y., NOVOTNY, V., MILLER, S. E. & PYLER, R. 2000. Quantifying biodiversity: experience with parataxonomists and digital photography in Papua New Guinea and Guyana. *BioScience*, 50, 899-908.
- BEDE, L. M., OSHIRO, L. M. Y., MENDES, L. M. D. & SILVA, A. A. 2008. Comparison of the population structure of the species of *Uca* (Crustacea: Decapoda: Ocypodidae)

- in the mangrove of Itacuruca, Rio Janeiro, Brazil. *Revista Brasileira de Zoologia*, 25, 601-607.
- BEHUM, M. E., BRODIE, R. J. & STATON, J. L. 2005. Distribution of juvenile *Uca pugnax* and *U. pugilator* across habitats in a South Carolina estuary, assessed by molecular techniques. *Marine Ecology Progress Series*, 288, 211-220.
- BELLWOOD, D. R., HOEY, A. S. & CHOAT, J. H. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters*, 6, 281-285.
- BERGEY, L. L. & WEIS, J. S. 2008. Aspects of population ecology in two populations of fiddler crabs, *Uca pugnax*. *Marine Biology*, 154, 435-442.
- BERTNESS, M. D. & MILLER, T. 1984. The distribution and dynamics of *Uca pugnax* (Smith) burrows in a New England salt marsh. *Journal of Experimental Marine Biology and Ecology*, 83.
- BLAKEWAY, D. R., ROBLES, C. D., FUENTES, D. A. & QIU, H. 2004. Spatially extensive, high resolution images of rocky shore communities. In: SEURONT, L. & STRUTTON, P. G. (eds.) *Handbook of scaling methods in aquatic ecology*. CRC Press.
- BOND, E. M. & CHASE, J. M. 2002. Biodiversity and ecosystem functioning at local and regional spatial scales. *Ecology Letters*, 5, 467-470.
- BOON, P. Y., YEO, D. C. J. & TODD, P. A. 2009. Sound production and reception in mangrove crabs *Perisesarma spp.* (Brachyura: Sesarmidae). *Aquatic Biology*, 5, 107-116.
- BOSIRE, J. O., KAIRO, J. G., KAZUNGU, J., KOEDAM, N. & DAHDOUH-GUEBAS, F. 2005. Predation on propagules regulates regeneration in a high-density reforested mangrove plantation. *Marine Ecology Progress Series*, 299, 149-155.
- BOTTO, F. & IRIBARNE, O. 2000. Contrasting effects of two burrowing crabs (*Chasmagnathus granulata* and *Uca uruguayensis*) on sediment composition and transport in estuarine environments. *Estuarine, Coastal and Shelf Science*, 51, 141-151.
- BOTTO, F., PALOMO, G., IRIBARNE, O. & MARTINEZ, M. M. 2000. The effect of Southwestern Atlantic burrowing crabs on habitat use and foraging activity of migratory shorebirds. *Estuaries* 23, 208-215.



- BOUILLON, S., CONNOLLY, R. M. & LEE, S. Y. 2008. Organic matter exchange and cycling in mangrove ecosystems: Recent insights from stable isotope studies. *Journal of Sea Research* 59, 44-58.
- BOUILLON, S., KOEDAM, N., RAMAN, A. V. & DEHAIRS, F. 2002. Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. *Oecologia*, 130, 441-448.
- BURGER, J., GOCHFELD, M., PLETNIKOFF, K., SNIGAROFF, R., SNIGAROFF, D. & STAMM, T. 2008. Ecocultural attributes: evaluating ecological degradation in terms of Ecological goods and services versus subsistence and tribal values. *Risk Analysis*, 28, 1261-1671.
- CANNICCI, S., BARTOLINI, F., DAHDOUH-GUEBAS, F., FRATINI, S., LITULO, C., MACIA, A., MRABU, E. J., PENHA-LOPES, G. & PAULA, J. 2009. Effects of urban wastewater on crab and mollusc assemblages in equatorial and subtropical mangroves of East Africa. *Estuarine, Coastal and Shelf Science*, 84, 305-317.
- CANNICCI, S., FRATINI, S. & VANNINI, M. 1999. Use of time, space and food resources in the mangrove climbing crab *Selatium elongatum* (Grapsidae, Sesamidae). *Marine Biology*, 135, 335-339.
- CANNICCI, S., RITOSSA, S., RUWA, R. K. & VANNINI, M. 1996a. Tree fidelity and hole fidelity in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae). *Journal of Experimental Marine Biology and Ecology*, 196, 299-311.
- CANNICCI, S., RUWA, R. K., GIUGGIOLI, M. & VANNINI, M. 1998. Predatory activity and spatial strategies of *Epixnathus dentatus* (Decapoda: Oziidae), an ambush predator among the mangroves. *Journal of Crustacean Biology*, 18, 57-63.
- CANNICCI, S. D.-G., F, ANYONA, D. & VANNINI, M. 1996b. Natural diet and feeding habits of *Thalamita crenata* (Decapoda: Portunidae). *Journal of Crustacean Biology*, 16, 678-683.
- CASTIGLIONI, D. D. S. & NEGREIROS-FRANSOZO, M. L. 2005. Comparative population biology of *Uca rapax* (Smith, 1870) (Brachyura, Ocypodidae) from two subtropical mangrove habitats on the Brazilian coast. *Journal of Natural History*, 39, 1627-1640.
- CHRISTY, J. H. & MORGAN, S. G. 1998. Estuarine immigration by crab postlarvae: mechanisms, reliability and adaptive significance. *Marine Ecology Progress Series*, 174, 51-65.

- COLBY, D. R. & FONSECA, M. S. 1984. Population dynamics, spatial dispersion and somatic growth of the sand fiddler crab *Uca pugilator*. *Marine Ecology Progress Series*, 16, 269-279.
- CONRAD, C. C. & HILCHEY, K. G. 2011. A review of citizen science and community-based environmental monitoring: issues and opportunities. *Environmental Monitoring and Assessment*, 176, 273-291.
- COOPER, C. B., DICKINSON, J., PHILLIPS, T. & BONNEY, R. 2007. Citizen science as a tool for conservation in residential ecosystems. *Ecology and Society*, 12, 11.
- COSTANZA, R., D'ARGE, R., DE GROOT, R., FARBERK, S., GRAZZO, M., HANNON, B., LIMBURG, K., NAEEM, S., O'NEILL, R. V., PARUELO, J., RASKIN, R. G., SUTTON, P. & VAN DEN BELT, M. 1997. The value of the world's ecosystem services and natural capital. *Nature*, 387, 253-260.
- COX, M. E., MOSS, A. & SMYTH, G. K. 2005. Water quality condition and trend in North Queensland waterways. *Marine Pollution Bulletin*, 51, 89-98.
- CRANE, J. 1975. Fiddler crabs of the world (Ocypodidae: *genus Uca*), Princeton University press.
- DAHDOUH-GUEBAS, F., GIUGGIOLI, M., OLUOCH, A., VANNINI, M. & CANNICCI, S. 1999. Feeding habits of non-Ocypidid crabs from two mangrove forests in Kenya. *Bulletin of Marine Science*, 64, 291-297.
- DAHDOUH-GUEBAS, F., VERNEIRT, M., CANNICCI, S., KAIRO, J. G., TACK, J. F. & KOEDAM, N. 2002. An exploratory study on grapsid crab zonation in Kenyan mangroves. *Wetlands Ecology and Management*, 10, 179-187.
- DAUVIN, J., BELLAN, G. & BELLAN, D. 2010. Bethic indicators: from subjectivity to objectivity - where is the line? *Marine Pollution Bulletin*, 60, 947-953.
- DE'ATH, G. 2002. Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology*, 83, 1105-1117.
- DELANEY, D. G., SPERLING, C. D., ADAMS, C. S. & LEUNG, B. 2008. Marine invasive species: validation of citizen science and implications for national monitoring networks. *Biological Invasions*, 10, 117-128.
- DESENDER, K., DEKONINCK, W., DUFRENE, M. & MAES, D. 2010. Changes in the distribution of carabid beetles in Belgium revisited: have we halted diversity loss? *Biological Conservation*, 143, 1549-1557.

- DICKINSON, J. L., SHIRK, J., BONTER, D., BONNEY, R., CRAIN, R. L., MARTIN, J., PHILLIPS, T. & PURCELL, K. 2012. The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment*, 10, 291-297.
- DUKE, N. C., MEYNECKE, J. O., DITTMANN, S., ELLISON, A. M., ANGER, K., BERGER, U., CANNICCI, S., DIELE, K., EWEL, K. C., FIELD, C. D., KOEDAM, N., LEE, S. Y., MARCHAND, C., NORDHAUS, I. & DAHDOUH-GUEBAS, F. 2007. A world without mangroves. *Science*, 317, 41-42.
- DURANT, J. M., HJERMANN, D. O., OTTERSEN, G. & STENSETH, N. C. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, 33, 271-283.
- DYE, A. H. & LASIAK, T. A. 1986. Microbenthos, meiobenthos and fiddler crabs: trophic interactions in a tropical mangrove sediment. *Marine Ecology Progress Series*, 32, 259-264.
- EMMERSON, W. D. 1994. Seasonal breeding cycles and sex ratios of eight species of crabs from Mgazana, a mangrove estuary in Transkei, Southern Africa. *Journal of Crustacean Biology*, 14, 568-578.
- ESCARPA, M., IRIBARNE, O. & NAVARRO, D. 2004. Effects of the intertidal burrowing crab *Chasmagnathus granulatus* on infaunal zonation patterns, tidal behavior, and risk of mortality. *Estuaries*, 27, 120-131.
- ESHKY, A. A., ATKINSON, R. J. A. & TAYLOR, A. C. 1995. Physiological ecology of crabs from Saudi Arabian mangrove. *Marine Ecology Progress Series*, 126, 83-95.
- EWA-OBOHO, I. O. 1993. Substratum preference of the tropical estuarine crabs, *Uca tangeri* Edoux (Ocypodidae) and *Ocypode cursor* Linne (Ocypodidae). *Hydrobiologia*, 271, 119-127.
- FAUSCH, K. D., TORGERSEN, C. E., BAXTER, C. V. & LI, H. W. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience*, 52, 483-498.
- FAUTH, P. T., GUSTAFSON, E. J. & RABENOLD, K. N. 2000. Using landscape metrics to model source habitat for Neotropical migrants in the midwestern U.S. *Landscape Ecology*, 15, 621-631.

- FENSHAM, R. J. & FAIRFAX, R. J. 2002. Aerial photography for assessing vegetation change: a review of applications and the relevance of findings for Australian vegetation history. *Australian Journal of Botany*, 50, 415-429.
- FIELDING, A. H. & BELL, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24, 38-49.
- FINCH, O. D., KRUMMEN, H., PLAISIER, F. & SCHULTZ, W. 2007. Zonation of spiders (Araneae) and carabid beetles (Coleoptera: Carabidae) in island salt marshes at the North Sea coast. *Wetlands Ecology and Management*, 15, 207-228.
- FRITH, D. & BRUNENMEISTER, S. 1980. Ecological and population studies of fiddler crabs (Ocypodidae, genus *Uca*) on a mangrove shore in Phuket Island, Western Penninsular Thailand. *Crustaceana*, 39, 157-184.
- FROST NERBONNE, J. N., K C 2008. Volunteer macroinvertebrate monitoring: tensions among group goals, data quality, and outcomes. *Environmental Management*, 42, 470-479.
- FRUSHER, S. D. 1988. Key to crabs associated with mangroves in North Queensland, Australian Institute of Marine Science.
- FRUSHER, S. D., GIDDINS, R. L. & SMITH, T. J. 1994. Distribution and abundance of Grapsid crabs (Grapsidae) in a mangrove estuary: effects of sediment characteristics, salinity tolerances, and osmoregulatory ability. *Estuaries*, 17, 647-654.
- GALLOWAY, A. W. E., TUDOR, M. T. & VANDER HAEGEN, M. W. 2006. The Reliability of citizen science: A case study of Oregon white oak stand surveys. *Wildlife Society Bulletin*, 34, 1425-1429.
- GEBAUER, P., PASCHKE, K. & ANGER, K. 1999. Costs of delayed metamorphosis: reduced growth and survival in early juvenile of an estuarine grapsid crab, *Chasmagnathus granulata*. *Journal of Experimental Marine Biology and Ecology*, 238, 271-281.
- GEBAUER, P., PASCHKE, K. & ANGER, K. 2002. Metamorphosis in a semiterrestrial crab, *Sesarma curcaoense*: intra- and interspecific settlement cues form adult odors. *Journal of Experimental Marine Biology and Ecology*, 268, 1-12.
- GEIST, S. J., NORDHAUS, I. & HINRICHS, S. 2011. Occurrence of species-rich crab fauna in a human-impacted mangrove forest questions the applications of

- community analysis as an environmental assessment tool. *Estuarine, Coastal and Shelf Science*, 1-12.
- GEORGE, S. B., CARLSON, M. D. & REGASSA, L. B. 2010. Shell use by juvenile fiddler crabs *Uca pugnax* and *U. pugilator*. *Journal of Experimental Marine Biology and Ecology*, 396, 35-41.
- GHERARDI, F. & RUSSO, S. 2001. Burrowing activity in the sand-bubbler crab, *Dotilla fenestrata* (Crustacea, Ocypodidae), inhabiting a mangrove swamp in Kenya. *Journal of Zoology*, 253, 211-223.
- GHERARDI, F., RUSSO, S. & LAZZARA, L. 2002. The function of wandering in the sand-bubbler crab, *Dotilla fenestrata*. *Journal of Crustacean Biology*, 22, 521-531.
- GIDDINS, R. L., LUCAS, J. S., NEILSON, M. J. & RICHARDS, G. N. 1986. Feeding ecology of the mangrove crab *Neosarmatium smithi* (Crustacea: Decapoda: Sesamidae). *Marine Ecology Progress Series*, 33, 147-155.
- GILBERT, B., SRIVASTAVA, S. & KIRBY, K. R. 2008. Niche partitioning at multiple scales facilitates coexistence among mosquito larvae. *Oikos*, 117, 944-950.
- GLASER, M. 2003. Interrelations between mangrove ecosystem, local economy and social sustainability in Caeté Estuary, North Brazil. *Wetlands Ecology and Management*, 11, 265-272.
- GLEASON, H. A. 1926. The individualistic concept of plant association. *Bulletin of the Torrey Botanical Club*, 53, 1-20.
- GODLEY, J. & BRODIE, R. 2007. Effect of summer storms on early life stage of *Uca minax*, *U. pugnax* and *U. pugilator* in North Inlet Estuary, South Carolina, USA. *Marine Ecology Progress Series*, 342, 197-204.
- GUEST, M. A., CONNOLLY, R. M., LEE, S. Y., LONERAGAN, N. R. & BREITFUSS, M. J. 2006. Mechanism for the small-scale movement of carbon among estuarine habitats: organic matter transfer not crab movement. *Oecologia* 148, 88-96.
- GUISAN, A. & ZIMMERMANN, N. E. 2000. Predictive habitat distribution models in ecology. *Ecological modelling*, 135, 147-186.
- GREENAWAY, P., MORRIS, S., MCMAHON, B. R., FARRELLY, C. A. & GALLAGHER, K. L. 1996. Air breathing by the purple shore crab, *Hemigrapsus nudus* (Dana). 1. Morphology, behaviour and respiratory gas exchange. *Physiological zoology*, 69, 785-805.

- HARTNOLL, R. G. 1973. Factors affecting the distribution and behaviour of the crab *Dotilla fenestrata* on East African shores. *Estuarine and Coastal Marine Science*, 1, 137-152.
- HARTNOLL, R. G., CANNICI, S., EMMERSON, W. D., FRATINI, S., MACIA, A., MGAYA, Y., PORRI, F., RUWA, R. K., SHUNULA, J. P. & SKOV, M. W. 2002. Geographic trends in mangrove crab abundance in East Africa. *Wetlands Ecology and Management*, 10, 203-213.
- HAWKINS, A. J. S. & JONES, M. B. 1982. Gill area and ventilation in two mud crabs, *Helice crassa* Dana (Grapsidae) and *Macrophthalmus hirtipes* Jacquinet (Ocypodidae), in relation to habitat. *Journal of Experimental Marine Biology and Ecology*, 60, 103-118.
- HEIKKINEN, R. K., LUOTO, M., VIRKKALA, R. & PEARSON, R. G. K., J 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology and Biogeography*, 16, 754-763.
- HEMMI, J. M., MARSHALL, J., PIX, W., VOROBYEV, M. & ZEIL, J. 2006. The variable colours of the fiddler crab *Uca vomeris* and their relation to background and predation. *The Journal of Experimental Biology*, 409, 4140-4153.
- HILTY, J. & MERENLENDER, A. 2000. Faunal indicator taxa selection for monitoring ecosystem health. *Biological Conservation*, 92, 185-197.
- HOLLIDAY, C. W. 1985. Salinity-induced changes in gill Na,K-ATPase activity in the mud fiddler crab, *Uca pugnax*. *The Journal of Experimental Zoology*, 233, 199-208.
- HOW, M. J., HEMMI, J. M., ZEIL, J. & PETERS, R. 2008. Claw waving display changes with receiver distance in fiddler crabs, *Uca perplexa*. *Animal Behaviour*, 75, 1015-1022.
- HSIEH, H., CHEN, C., CHEN, Y. & YANG, H. 2002. Diversity of benthic organic matter flows through polychaetes and crabs in a mangrove estuary:  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  signals. *Marine Ecology Progress Series*, 227, 145-155.
- HUBBELL, S. P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs*, 16, S9-S21.
- ICELY, J. D. & JONES, D. A. 1978. Factors affecting the distribution of the genus *Uca* (Crustacea: Ocypodidae) on an East African shore. *Estuarine and Coastal Marine Science*, 6, 315-325.

- IKEDA, H., KUBOTA, K., KAGAWA, A. & SOTA, T. 2010. Diverse diet compositions among harpaline ground beetle species revealed by mixing model analyses of stable isotope ratios. *Ecological Entomology*, 35, 307-316
- IRMLER, U., HELLER, K., MEYER, H. & REINKE, H. 2002. Zonation of ground beetles (Coleoptera: Carabidea) and spiders (Araneida) in salt marshes at the North and Baltic Sea and the impact of the predicted sea level increase. *Biodiversity and Conservation*, 11, 1129-1147.
- JAROENSUTASINEE, M. & JAROENSUTASINEE, K. 2004. Morphology, density, and sex ration of fiddler crabs from Southern Thailand (Decapoda, Brachyura, Ocypodidae). *Crustaceana*, 77, 533-551.
- JONES, M. B. 1976. Limiting factors in the distribution of intertidal crabs (Crustacea: Decapoda) in the Avon-Heathcote estuary, Christchurch. *New Zealand Journal of Marine and Freshwater Research* 10, 577-587.
- JONES, M. B. & GREENWOOD, J. G. 1982. Water loss of a porcelain crab *Petrolisthes elongatus* (Mile Edwards, 1837) (Decapoda, anomura) during atmospheric exposure. *Comparative Biochemistry and Physiology Part A: Physiology*, 72.
- JONES, M. B. & SIMONS, M. J. 1982. Habitat preferences of two estuarine burrowing crabs *Helice crassa* Dana (Grapsidae) and *Macrophthalmus hirtipes* (Jaquinot) (Ocypodidae). *Journal of Experimental Marine Biology and Ecology*, 56, 49-62.
- JORDÃO, J. M. & OLIVEIRA, R. F. 2003. Comparison of non-invasive methods for quantifying population density of the fiddler crab *Uca tangeri*. *Journal of the Marine Biological Association of the UK*, 83, 981-982.
- KANAYA, G., TAKAGI, S. & KIKUCHI, E. 2008. Dietary contribution of the microphytobenthos to infaunal deposit feeders in an estuarine mudflat in Japan. *Marine Biology*, 155, 543-553.
- KNEIB, R. T. & WEEKS, C. A. 1990. Intertidal distribution and feeding habits of the mud crab, *Eurytium limosum*. *Estuaries*, 13, 462-468.
- KNOPF, G. N. 1966. Observations on behavioral ecology of the fiddler crab, *Uca pugilator* (Bosc). *Crustaceana*, 11, 302-306.
- KOCH, V. & WOLFF, M. 2002. Energy budget and ecological role of mangrove epibenthos in the Caeté estuary, North Brazil. *Marine Ecology Progress Series*, 228, 119-130.

- KOCH, V., WOLFF, M. & DIELE, K. 2005. Comparative population dynamics of four fiddler crabs (Ocypodidae, genus *Uca*) from a North Brazilian mangrove ecosystem *Marine Ecology Progress Series*, 291, 177-188.
- KOGA, T. 1995. Movements between microhabitats depending on reproduction and life history in the sand-bubbler crab *Scopimera globosa*. *Marine Ecology Progress Series*, 117, 65-74.
- KON, K., HOSHINO, Y., KANOU, K., OKAZAKI, D., NAKAYAMA, S. & KOHNO, H. 2012. Importance of allochthonous material in benthic macrofaunal community functioning in estuarine salt marshes. *Estuarine, Coastal and Shelf Science*, 96, 236-244.
- KON, K., KUROKURA, H. & HAYASHIZAKI, K. 2007. Role of microhabitats in food webs of benthic communities in a mangrove forest. *Marine Ecology Progress Series*, 340, 55-62.
- KRISTENSEN, D. K., KRISTENSEN, E. & MANGION, P. 2010. Food partitioning of leaf-eating mangrove crabs (*Sesarminae*): experimental and stable isotope ( $^{13}\text{C}$  and  $^{15}\text{N}$ ) evidence. *Estuarine, Coastal and Shelf Science*, 87, 583-590.
- KRISTENSEN, E. 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. *Journal of Sea Research*, 59, 30-43.
- KYOMO, J. 1986. reproductive activities in the sesarmid crab *Sesarma intermedia* in the coastal and estuarine habitats of Hakata, Japan. *Marine Biology*, 91, 319-329.
- LAYNE, J. E., JON, W., BARNES, P. & DUNCAN, L. M. J. 2003. Mechanisms of homing in the fiddler crab *Uca rapax* 2. Information sources and frame of reference for a path integration system. *The Journal of Experimental Biology*, 206, 4425-4442.
- LECOMTE, F. & DODSON, J. J. 2004. Role of early life-history constraints and resource polymorphism in the segregation of sympatric populations of an estuarine fish. *Evolutionary Ecology Research*, 6, 631-658.
- LEE, S. Y. 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. *Marine and Freshwater Research*, 49, 335-343.
- LEE, S. Y. 2008. Mangrove macrobenthos: assemblages, services, and linkages. *Journal of Sea Research*, 59, 16-29.
- LEE, S. Y., DUNN, R. J. K., YOUNG, R. A., CONNOLLY, R. M., DALE, P. E. R., DEHAYR, R., LEMCKERT, C. J., MCKINNON, S., POWELL, B., TEASDALE, P. R. &



- WELSH, D. T. 2006. Impact of urbanization on coastal wetland structure and function. *Australian Ecology*, 31, 149-163.
- LEE, S. Y. & Kwok, P. W. 2002. The importance of mangrove species association to the population biology of two sesarminae crabs, *Perisesarma bidens* and *Parasesarma affinis*. *Wetland Ecology and Management*, 10, 215-226.
- LEVIN, L. A. 2006. Recent progress in understanding larval dispersal: new direction and digressions. *Integrative and Comparative Biology*, 46, 282-297.
- LIM, S. & KALPANA, S. 2011. Maxilliped-setation adaptations to habitat and sexual dimorphism of feeding claws in *Uca perplexa* and *U. vomeris*. *Journal of Crustacean Biology*, 31, 406-412.
- LIM, S. S. L. & HENG, M. S. 2007. Mangrove micro-habitat influence on bioturbative activities and burrow morphology of the fiddler crab, *Uca annulipes* (H. Milne Edwards, 1837) (Decapoda, Ocypodidae). *Crustaceana*, 80, 31-45.
- LOVELOCK, C. E. & ELLISON, J. 2007. Vulnerability of mangroves and tidal wetlands of the Great Barrier Reef to climate change. *Climate change and the Great barrier reef: a vulnerability assessment*.
- MACIA, A., QUINCARETE, I. & PAULA, J. 2001. A comparison of alternative methods for estimating population density of the fiddler crab *Uca annulipes* at Saco mangrove, Inhaca Island (Mozambique). *Hydrobiologia*, 449, 213-219.
- MACINTOSH, D. J., ASHTON, E. C. & HAVANON, S. 2002. Mangrove rehabilitation and intertidal biodiversity: a study in the ranong mangrove ecosystem, Thailand. *Estuarine, Coastal and Shelf Science*, 55, 331-345.
- MAITLAND, D. P. 1990. Carapace and branchial water circulation, and water-related behaviours in the semaphore crab *Helioecius cordiformis* (Decapod: Brachyura: Ocypodidae). *Marine biology*, 105, 275-286.
- MARTIN, T. E. 2007. Climate correlates of 20 years of trophic changes in a high-elevation riparian system. *Ecology*, 88, 367-380.
- MARTINETTO, P., PALOMO, G., BRUSCHETTI, M. & IRIBARNE, O. 2011. Similar effects on sediment structure and infaunal community of two competitive intertidal soft-bottom burrowing crab species. *Journal of the Marine Biological Association of the UK*, 91, 1385-1393.

- MARTINUZZI, S., GOULD, W. A., LUGO, A. E. & MEDINA, E. 2009. Conversion and recovery of Puerto Rican mangroves: 200 years of change. *Forest Ecology and Management*, 257.
- MAZUMDER, D. & SAINTILAN, N. 2010. Mangrove leaves are not an important source of dietary carbon and nitrogen for crabs in temperate Australian mangroves. *Wetlands*, 30, 375-380.
- MCGAW, I. J. 2001. Impacts of habitat complexity on physiology: purple shore crabs tolerate osmotic stress for shelter. *Estuarine, Coastal and Shelf Science*, 53, 865-876.
- MCGAW, I. J., REIBER, C. L. & GUADAGNOLI, J. A. 1999. Behavioral physiology of four crab species in low salinity. *Biological bulletin*, 196, 163-176.
- MCHENGA, I. S. S. & TSUCHIYA, M. 2008. Nutrient dynamics in mangrove crab burrow sediments subjected to anthropogenic input. *Journal of Sea Research*, 59, 103-113.
- MCIVOR, C. C. & SMITH, T. J. 1995. Differences in the crab fauna of mangrove areas at a Southwest Florida and a Northeast Australia location: implications for leaf litter processing. *Estuaries*, 18, 591-597.
- MEZIANE, T., D'AGATA, F. & LEE, S. Y. 2006. Fate of mangrove organic matter along a subtropical estuary. *Marine Ecology Progress Series*, 312, 15-27.
- MEZIANE, T., SANABE, M. C. & TSUCHIYA, M. 2002. Role of fiddler crabs of a subtropical intertidal flat on the fate of sedimentary fatty acids. *Journal of Experimental Marine Biology and Ecology*, 270, 191-201.
- MICHELI, F. 1993. Feeding ecology of mangrove crabs in North Eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithi*. *Journal of Experimental Marine Biology and Ecology*, 171, 165-186.
- MICHELI, F., GHERARDI, F. & VANNINI, M. 1991. Feeding and burrowing ecology of two East African mangrove crabs. *Marine Biology*, 111, 247-254.
- MILLER, K. G. & MAUER, D. 1973. Distribution of the fiddler crabs, *Uca pugnax* and *Uca minax*, in relation to salinity in Delaware rivers. *Chesapeake Science*, 14, 219-221.
- MILLER-RUSHING, A., PRIMACK, R. & BONNEY, R. 2012. The history of public participation in ecological research. *Frontiers in Ecology and the Environment*, 10, 285-290.

- MISTRI, M., FANO, E. A. & ROSSI, R. 2001. Redundancy of macrobenthos from lagoonal habitats in the Adriatic Sea. *Marine Ecology Progress Series*, 215, 289-296.
- MORLEY, S. A., TOFT, J. D. & HANSON, K. M. 2012. Ecological effects of shoreline armoring on intertidal habitats of a Puget Sound urban estuary. *Estuaries and Coasts*, 35, 774-784.
- MORRIS, D. W. 1996. Coexistence of specialist and generalist rodents via habitat selection. *Ecology*, 77, 2352-2364
- MOSS, A., BRODIE, J. & FURNAS, M. 2005. Water quality guideline for the Great Barrier Reef World Heritage Area: a basis for development and preliminary values. *Marine Pollution Bulletin*, 51, 76-88.
- MOUTON, E. C., JR. & FELDER, D. L. 1996. Burrow distributions and population estimates for the fiddler crabs *Uca spinicarpa* and *Uca longisignalis* in a Gulf of Mexico salt marsh. *Estuaries*, 19, 51-61.
- MURAI, M., GOSHIMA, S. & NAKASONE, Y. 1982. Some behavioural characteristics related to food supply and soil texture of burrowing habitats observed on *Uca vocans vocans* and *U. lactea perplexa*. *Marine Biology* 66, 191-197.
- NAGELKERKEN, I., BLABER, S. J. M., BOUILLON, S., GREEN, P., HAYWOOD, M., KIRTON, L. G., MEYNECKE, J. O., PAWLIK, J., PENROSE, H. M., SASEKUMAR, A. & SOMERFIELD, P. J. 2008. The habitat function of mangroves for terrestrial and marine fauna. *Aquatic Botany* 89, 155-185.
- NESS, E. G. 1972. A survey of the Anomura and Brachyura of the Ross River estuary, Townsville. Bsc Hons., James Cook University.
- NETO, J. M., TEIXEIRA, H., PATRICIO, J., BAETA, A., VERISSIML, H., PINTO, R. & MARQUES, J. C. 2010. The response of estuarine macrobenthic communities to natural- and human-induced changes: dynamics and ecological quality. *Estuaries and Coasts*, 33, 1327-1339.
- NEWMAN, G., WIGGINS, A., CRALL, A., GRAHAM, E., NEWMAN, S. & CROWSTON, K. 2012. The future of citizen science: emerging technologies and shifting paradigms. *Frontiers in Ecology and the Environment*, 10, 298-304.
- NG, P. K. L., GUINOT, D., DAVIE, P. J. F. 2008. Systema Brachyurorum: Part I. An annotated checklist of extant Brachyuran crabs of the world. *The Raffles Bulletin of Zoology*, 17, 1-286.

- NOBBS, M. 2003. Effects of vegetation differ among three species of fiddler crabs (*Uca* spp.). *Journal of Experimental Marine Biology and Ecology*, 284, 41-50.
- NOBBS, M. & MCGUINNESS, K. A. 1999. Developing methods for quantifying the apparent abundance of fiddler crabs (Ocypodidae: *Uca*) in mangrove habitats. *Australian Journal of Ecology* 24, 43-49.
- NORDHAUS, I. 2004. Feeding ecology of the semi-terrestrial crab *Ucides cordatus cordatus* (Decapoda: Brachyura) in a mangrove forest in northern Brazil. *ZMT Contributions*, 18, 1-198.
- NORDHAUS, I., SALEWSKI, T. & JENNERJAHN, T. C. 2011. Food preferences of mangrove crabs related to leaf nitrogen compounds in the Segara Anakan Lagoon, Java, Indonesia. *Journal of Sea Research*, 65, 414-426.
- NORDHAUS, I., WOLFF, M. & DIELE, K. 2006. Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. *Estuarine Coastal and Shelf Science*, 67, 239-250.
- O'CONNOR, N. J. & VAN, B. T. 2006. Adult fiddler crabs *Uca pugnax* (Smith) enhance sediment-associated cues for molting of conspecific megalopae. *Journal of Experimental Marine Biology and Ecology*, 335, 123-130.
- OTANI, S., KOZUKI, Y., YAMANAKA, R., SASAOKA, H., ISHIYAMA, T., YOKITSU, Y., SAKAI, H. & FUJIKI, Y. 2010. The role of crabs (*Macrophthalmus japonicus*) burrows on organic carbon cycle in estuarine tidal flat, Japan. *Estuarine, Coastal and Shelf Science*, 86, 434-440.
- PENHA-LOPES, G., BARTOLINI, F., LIMBU, S., CANNICCI, S., KRISTENSEN, E. & PAULA, J. 2009a. Are fiddler crabs potentially useful ecosystem engineers in mangrove wastewater wetlands. *Marine Pollution Bulletin*, 58, 1694-1703.
- PEREZ, D. M., ROSENBERG, M. S. & PIE, M. R. 2012. The evolution of waving displays in fiddler crabs (*Uca* spp., Crustacea: Ocypodidae). *Biological Journal of the Linnean Society*, 106, 307-315.
- POON, D. Y. N., CHAN, B. K. K. & WILLIAMS, G. A. 2010. Spatial and temporal variation in diets of the crabs *Metopograpsus frontalis* (Grapsidae) and *Perisesarma bidens* (Sesamidae): implications for mangrove food webs. *Hydrobiologia* 638, 29-40.
- POPPER, A. N., SALMON, M. & HORCH, K. W. 2001. Acoustic detection and communication by decapod crustaceans. *Journal of Comparative Physiology A*, 187, 83-89.

- POTTS, M. D., DAVIES, S. J., BOSSERT, W. H., TAN, S. & SUPARDI, M. N. 2004. Habitat heterogeneity and niche structure of trees in two tropical rain forests. *Oecologia*, 139, 446-453.
- POWERS, L. W. & COLE, J. F. 1976. Temperature variation in fiddler crab microhabitats. *Journal of Experimental Marine Biology and Ecology*, 21, 141-157.
- RABALAIS, N. N. & CAMERON, J. N. 1985. Physiological and morphological adaptations of adult *Uca subcylindrica* to semi-arid environments. *The Biological Bulletin*, 168, 135-146.
- RAVICHANDRAN, S., ANTHONISAMY, S., KUANNUPANDI, T. & BALASUBRAMANIAN, T. 2007. Habitat preference of crabs in Pichavaram mangrove environment, Southeast coast of India. *Journal of Fisheries and Aquatic Science*, 2, 47-55.
- RAYMOND, C. M., BRYAN, B. A., MACDONALD, D. H., CAST, A., STRATHEARN, S., GRANDGIRARD, A. & KALIVAS, T. 2009. Mapping community values for natural capital and ecosystem services. *Ecological Economics*, 68, 1301-1315.
- RIBEIRO, P. D., IRIBARNE, O. O., JAUREGUY, L., NAVARRO, D. & BOGAZZI, E. 2003. Variable sex-specific mortality due to shorebird predation on a fiddler crab. *Canadian Journal of Zoology*, 81, 1209-1221
- ROBERTSON, J. R., FUDGE, J. A. & VERMEER, G. K. 1981. Chemical and live feeding stimulants of the sand fiddler crab, *Uca pugilator* (Bosc.). *Journal of Experimental Marine Biology and Ecology*, 53.
- RONNBACK, P. 1999. The ecological basis for economic value of seafood production supported by mangrove ecosystems. *Ecological Economics* 29, 235-252.
- RONNBACK, P. 2001. Ecological economics of fisheries supported by mangrove ecosystems: economic efficiency, mangrove dependence, sustainability and benefit-transfer. *2nd Western Indian Ocean Science Association (WIOMSA) Scientific Symposium -Book of Abstracts*, 41.
- SAINTILAN, N. & MAZUMDER, D. 2010. Fine-scale variability in the dietary sources of grazing invertebrates in a temperate Australian saltmarsh. *Marine and Freshwater Research*, 61, 615-620.
- SALGADO KENT, S. P. & MCGUINNESS, K. A. 2006. A comparison of methods for estimating relative abundance of grapsid crabs. *Wetlands Ecology and Management*, 14, 1-9.

- SASEKUMAR, A. 1974. Distribution of macrofauna on a Malayan mangrove shore *Journal of Animal Ecology*, 43, 51-69.
- SCHWARTZ, M. W., BRIGHAM, C. A., HOEKSEMA, J. D., LYONS, K. G., MILLS, M. H. & VAN MANTEGEM, P. J. 2000. Linking biodiversity to ecosystem function: implications for conservation biology. *Oecologia*, 122, 297-305.
- SEIPLE, W. 1979. Distribution, habitat preference and breeding periods in the crustaceans *Sesarma cinereum* and *S. reticulatum* (Brachyura: Decapoda: Grapsidae). *Marine Biology*, 52, 77-86.
- SETO, K. C. 2011. Exploring the dynamics of migration to mega-delta cities in Asia and Africa: Contemporary drivers and future scenario. *Global Environmental Change*, 21S, 94-107.
- SHAW, M. & TIBBETTS, I. R. 2004. Grazing by *Metopograpsus frontalis* (Decapoda: Grapsidae) on intertidal rock walls of Moreton Bay. *Proceedings of the Royal Society of Queensland*, 111, 95-101.
- SHEAVES, M. 2005. Nature and consequences of biological connectivity in mangrove systems. *Marine Ecology Progress Series*, 302, 293-305.
- SHEAVES, M. & JOHNSTON, R. 2009. Ecological drivers of spatial variability among fish fauna of 21 tropical Australian estuaries. *Marine Ecology Progress Series*, 385, 245-260.
- SHEAVES, M. & JOHNSTON, R. 2010. Implications of spatial variability of fish assemblages for monitoring of Australia's tropical estuaries. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 20, 348-356.
- SHEAVES, M., JOHNSTON, R. & CONNOLLY, R. M. 2010. Temporal dynamics of fish assemblages of natural and artificial tropical estuaries. *Marine Ecology Progress Series*, 410, 143-157.
- SHEAVES, M. & MOLONY, B. 2000. Short-circuit in the mangrove food chain. *Marine Ecology Progress Series*, 199, 97-109.
- SIEGEL, S. & CASTELLAN, N. J. 1988. *Nonparametric Statistics for the Behavioral Sciences*, New York, McGraw-Hill.
- SILVERTOWN, J. 2009. A new dawn for citizen science. *Trends in Ecology and Evolution*, 24, 467-471.

- SIMITH, D. & DIELE, K. 2008. The effect of salinity on the larval development of the Uca crab, *Ucides cordatus* (Linnaeus, 1763) (Decapoda: Ocypodidae) in Northern Brazil. *Acta Amazonica*, 38, 345-350.
- SIRAJUL, I. M. D., SHIGEMITSU, S., TAKASHI, N., MOHAMMED, S., YOSHIHISA, F. & TOHRU, N. 2003. Distribution and abundance of crustaceans in the Shira River mangrove swamp at Iriomote Island of Okinawa in Japan. *Bulletin of the Faculty of Science University of the Ryukyus* 76, 227-244.
- SIVASOTHI, N. 2000. Niche preferences of tree-climbing crabs in Singapore mangroves. *Crustaceana*, 73, 25-38.
- SKILLETER, G. A. & WARREN, S. 2000. Effects of habitat modification in mangroves on the structure of mollusc and crab assemblages. *Journal of Experimental Marine Biology and Ecology*, 244, 107-129.
- SKOV, M. W. & HARTNOLL, R. G. 2002. Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves? *Oecologia*, 131, 1-7.
- SKOV, M., VANNINI, M., SHUNULA, J., HARTNOLL, R. & CANNICCI, S. 2002. Quantifying the density of mangrove crabs: Ocypodidae and Grapsidae. *Marine Biology*, 141, 725-732.
- SMITH, T. J., BOTO, K. G., FRUSHER, S. D. & GIDDINS, R. L. 1991. Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. *Estuarine, Coastal and Shelf Science*, 33, 419-432.
- SNELLING, B. 1958. The distribution of intertidal crabs in the Brisbane River. *Australian Journal of Marine and Freshwater Research* 10, 67-83.
- SOLAN, M., GERMANO, J. D., RHOADS, D. C., SMITH, C., MICHAUD, E., PARRY, D., WENZHOFFER, R., KENNEDY, B., HENRIQUES, C., BATTLE, E., CAREY, D., IOCCO, L., VALENTE, R., WATSON, J. & ROSENBERG, R. 2003. Towards a greater understanding of pattern, scale and process in marine benthic systems: a picture is worth a thousand worms. *Journal of Experimental Marine Biology and Ecology*, 285-286, 313-338.
- TAKAGI, K. K., CHERDSUKJAI, P., MIMURA, I., YANO, Y., ADULYANUKOSOL, K. & TSUCHIYA, M. 2010. Soldier crab (*Dotilla myctiroides*) distribution, food resources and subsequent role in organic matter fate in Ao Tang Khen, Phuket, Thailand. *Estuarine, Coastal and Shelf Science*, 2010, 611-617.

- TAKEDA, S. 2010. Habitat partitioning between prey soldier crab *Mictyris brevidactylus* and predator fiddler crabs *Uca perplexa*. *Journal of Experimental Marine Biology and Ecology*, 390, 160-168.
- TEAL, J. M. 1958. Distribution of fiddler crabs in Georgia Salt marshes. *Ecology*, 39, 186-193.
- TILMAN, D. 1982. *Resource competition and community structure*, Princeton, N.J., Princeton University Press.
- TOPPING, C. J. & SUNDERLAND, K. D. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of Winter Wheat. *Journal of Applied Ecology*, 29, 485-491.
- TURNER, T. F., COLLYER, M. L. & KRABBENHOFT, T. J. 2010. A general hypothesis-testing framework for stable isotope ratios in ecological studies. *Ecology*, 91, 2227-2233.
- VALIELA, I., BOWEN, J. L. & YORK, J. K. 2001. Mangrove Forests: one of the world's threatened major tropical environments. *BioScience*, 51, 807-815.
- VERGAMINI, F. G. & MANTELATTO, F. L. 2008. Microdistribution of juveniles and adults of the mud crab *Panopeus americanus* (Brachyura, Panopeidae) in a remnant mangrove area in the southwest Atlantic. *Journal of Natural History*, 42, 1581-1589.
- VON HAGEN, H. 1993. Waving display in females of *Uca polita* and of other Australian fiddler crabs. *Ethology*, 93, 3-20.
- WARNER, G. F. 1969. The occurrence and distribution of crabs in a Jamaican mangrove swamp. *Journal of Animal Ecology*, 38, 379-389.
- WARREN, J. H. 1990. The use of open burrows to estimate abundances of intertidal estuarine crabs. *Australian Ecology*, 15, 277-280.
- WEIS, J. S. & WEIS, P. 2004. Behaviour of four species of fiddler crabs, genus *Uca*, in Southeast Sulawesi, Indonesia. *Hydrobiologia*, 523, 47-58.
- WEISBERG, S. B. & RANASINGHE, J. A. 1997. An estuarine benthic index of biotic integrity (B-IBI) for Chesapeake Bay. *Estuaries*, 20, 149-158.
- WENTWORTH, C. K. 1922. A scale of grade and class terms for clastic sediments. *The Journal of Geology*, 30, 377-392.







- WERRY, J. & LEE, S. Y. 2005. Graspid carbs mediate link between mangrove litter production and estuarine planktonic food chains. *Marine Ecology Progress Series*, 293, 165-176.
- WHITFIELD, J. 2002. Ecology: neutrality versus the niche. *Nature*, 417, 480-481.
- WHITTAKER, R. H. 1975. *Communities and Ecosystems*, MacMillan, New York.
- WINDER, M. & SCHINDLER, D. E. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology*, 85, 2100-2116.
- WINTLE, B. A., ELITH, J. & POTTS, J. M. 2005. Fauna habitat modelling and mapping: a review and case study in the Lower Hunter Central Coast region of NSW. *Australian Ecology*, 30, 719-738.
- WOLFF, M., KOCH, V. & ISAAC, V. 2000. A trophic flow model of the Caeté Mangrove Estuary (North Brazil) with considerations for the sustainable use of its resources. *Estuarine, Coastal and Shelf Science* 50, 786-803.
- WOLFRATH, B. 1993. Observations on the behaviour of the European fiddler crab *Uca tangeri*. *Marine Ecology Progress Series*, 100, 111-118.
- YOKOYAMA, H., TAMAKI, A., HARADA, K., SHIMODA, K., KOYAMA, K. & ISHIHI, Y. 2005. Variability of diet-tissue isotopic fractionation in estuarine macrobenthos. *Marine Ecology Progress Series*, 296, 115-128.
- ZEIL, J. 1998. Homing of fiddler crabs (*Uca lactea annulipes* and *Uca vomeris*: Ocypodidae). *Journal of Comparative Physiology A* 183, 367-377.
- ZEIL, J. & HEMMI, J. M. 2006. The visual ecology of fiddler crabs. *Journal of Comparative Physiology*, 192, 1-25.

# Appendix 1: ID-sheet for common crabs of the low intertidal zone













## ID-sheet for common crabs on low intertidal banks

Peter Vermeiren 2012

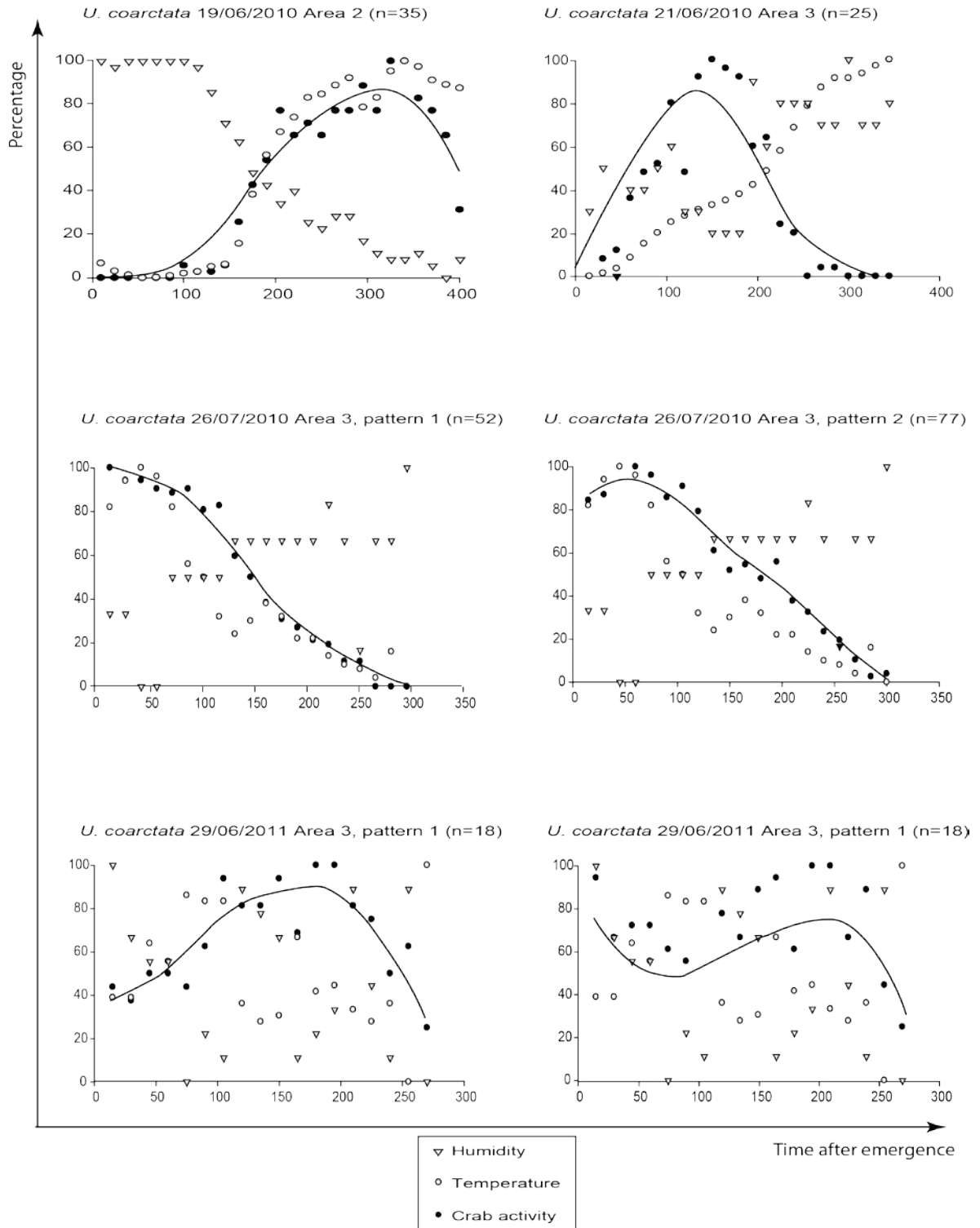
### Grapsoidea

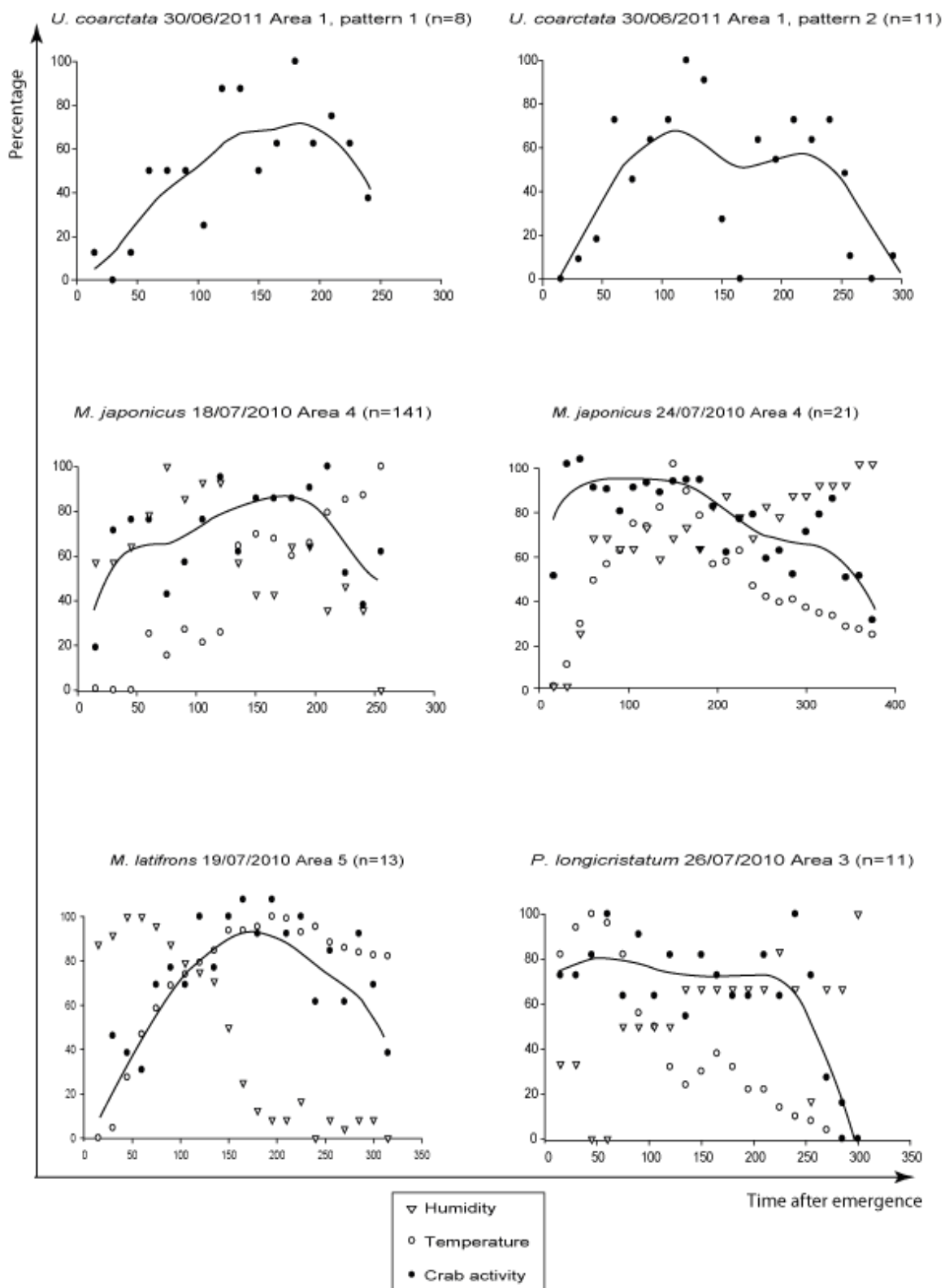
			
<i>Metopograpsus frontalis</i>	<i>Metopograpsus thukuhar</i>	<i>Metopograpsus latifrons</i>	<i>Perisesarma longicristatum</i>

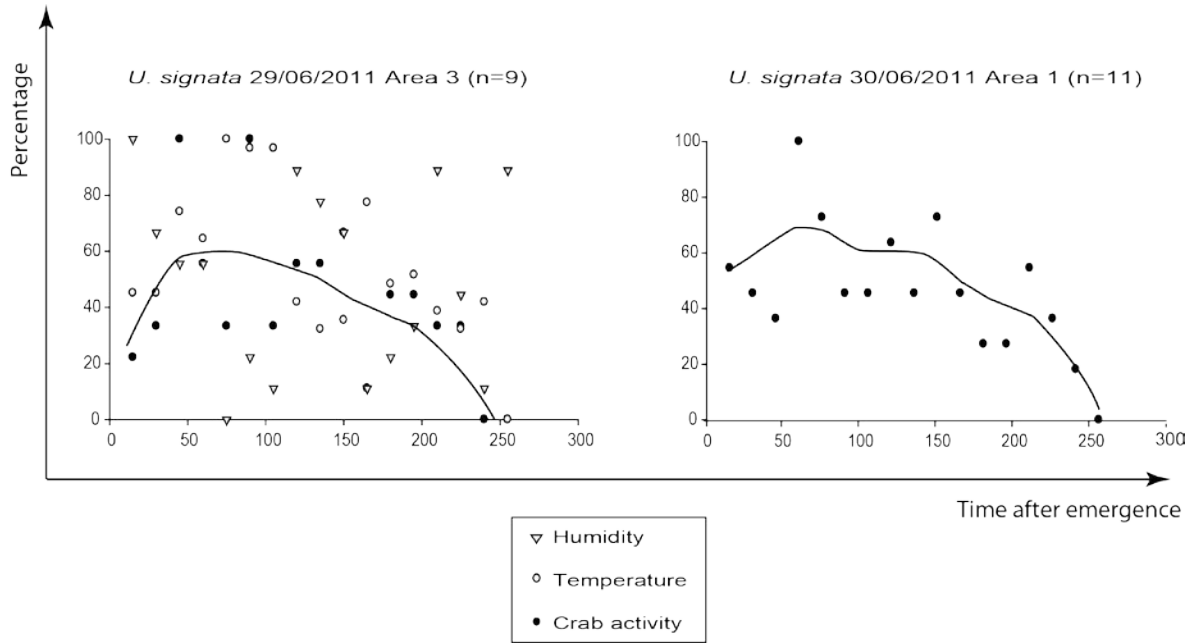
### Ocypodoidea

			
<i>Uca vomeris</i>	<i>Uca signata</i>	<i>Ocypode ceratophthalma</i>	<i>Dotilla fenestrata</i>
			
<i>Uca seismella</i>	<i>Australoplax tridentata</i>	<i>Mictyris longicarpus</i>	<i>Ilyoplax dentata</i>
		<p>ID based on Frusher 1988                      Note: colors may vary. Identification is best for adult intertidal crabs</p> <p>Photos:                      P. Vermeiren, M. Sheaves (<i>U. signata</i>), K. Vermeiren (<i>O. ceratophthalma</i>), A. Verheyden (<i>D. fenestrata</i>), Frusher 1988 (<i>U. perplexa</i>), Kitaura 2006 (<i>I. dentata</i>), J. collins (<i>S.s. longicristatum</i>)</p> <p>Contact: <a href="mailto:peter.vermeiren@my.jcu.edu.au">peter.vermeiren@my.jcu.edu.au</a></p>	
<i>Uca coarctata</i>	<i>Macrophthalmus japonicus</i>		
			
<i>Uca perplexa</i>	<i>Cleistostoma wardi</i>		

## Appendix 2: Surface activity patterns of intertidal crabs





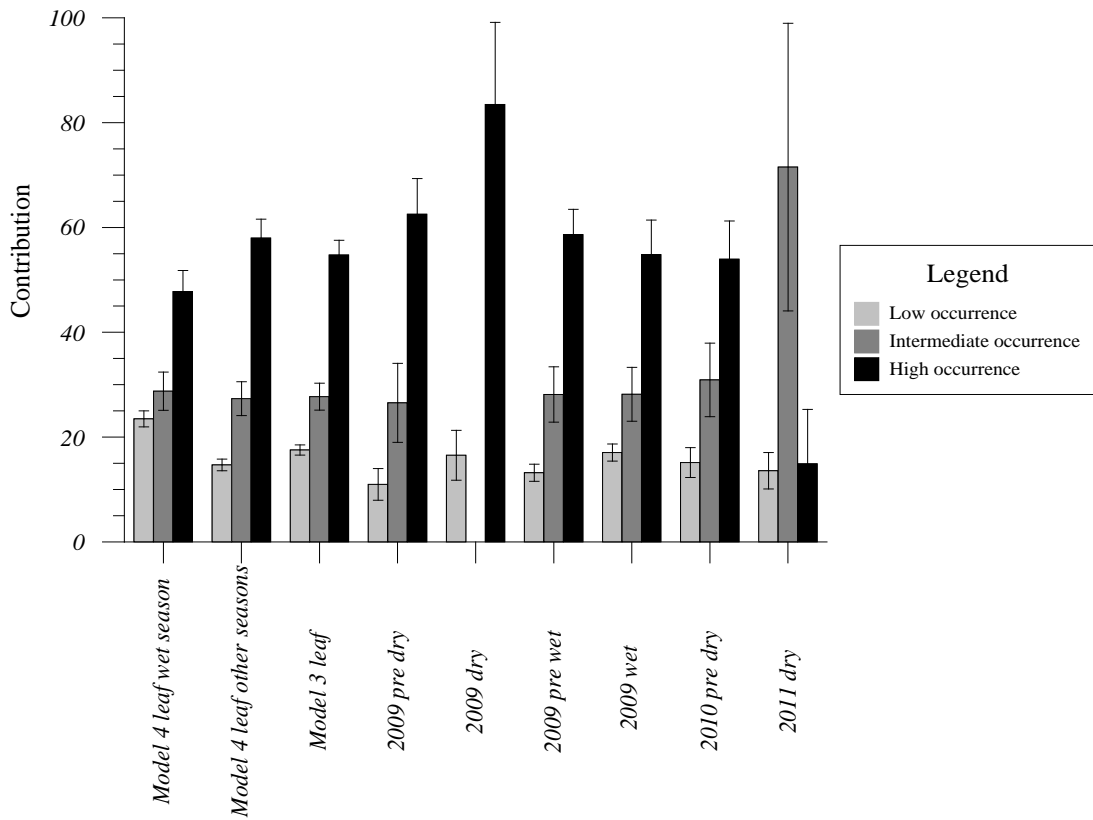


**Figure A2.1** Patterns in abundance of intertidal crabs and in temperature and humidity levels over time after emergence of their habitat. All values were standardized relative to the lowest value recorded and expressed as a percentage relative to the highest value recorded for crab abundance, temperature and humidity. Data on crab abundance were visualized with a distance weighted least squares smoothing function.

## **Appendix 3: Additional details of the CART models of habitat association of intertidal crabs in Stuart Creek (Chapter 5)**

### **A3.1: Details on the CART model of *U. coarctata***

A four leaf model for relative occurrence of *U. coarctata* was developed using CART analysis. However, this model proposed a seasonal split between wet seasons and other seasons, which could only be tested with data from one test trip: the 2009 wet season. Additionally, in the 2009 wet season trip the pattern of contributions of the relative occurrence across the predicted clusters resembled the pattern of contribution observed in the training data not including the wet season data, more than the pattern observed for the wet season training data (Fig. A3.1). Reducing the CART model to three leaves by disregarding the seasonal split, improves the misclassification error for the 2009 wet season test trip while misclassification errors for the training data and the remaining five test trips only increased slightly (Table A3.1). In conclusion, this three leaf model (Fig. 5.3 in the main text) was considered more robust given the available data.



**Figure A3.1** Percentage contribution of the relative occurrence of *U. coarctata* in each cluster relative to the total relative occurrence across all clusters per trip ( $\pm$ SE) in the training and test trips

**Table A3.1** Misclassification errors of the within-site CART models of *U. coarctata*

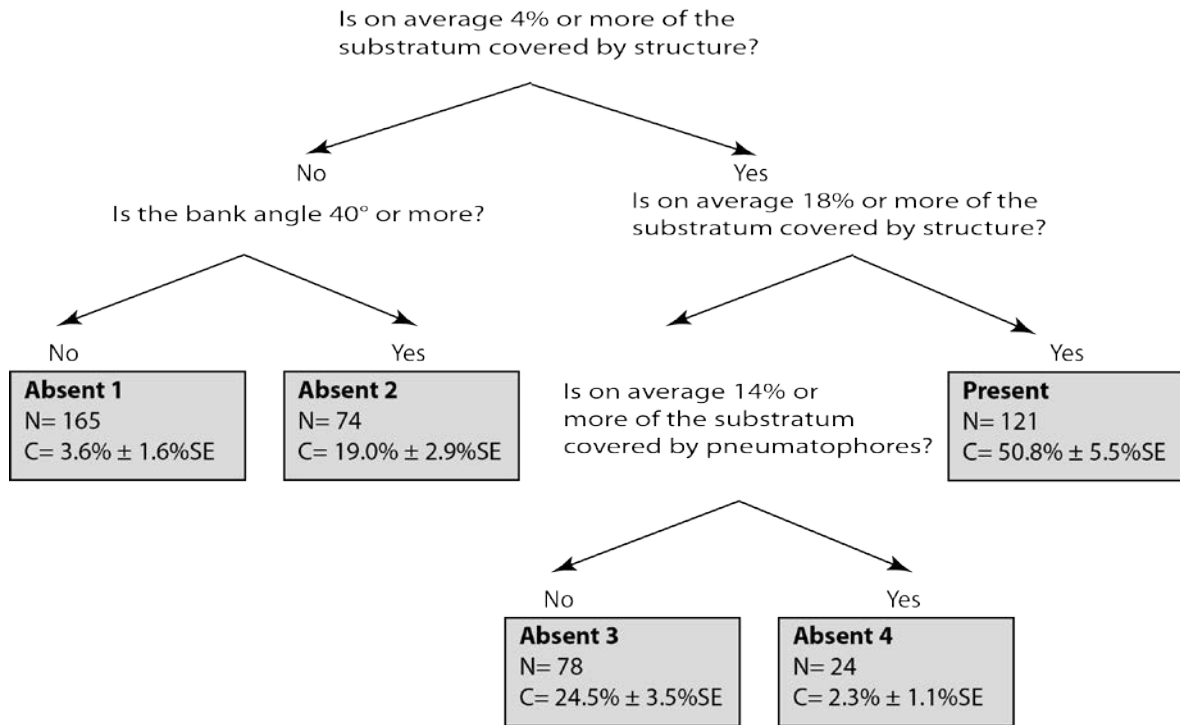
Trip	4 leaf	3 leaf
<b>2009 pre dry</b>	0.012939	0.014279
<b>2009 dry</b>	0.019137	0.022657
<b>2009 pre wet</b>	0.008657	0.009754
<b>2009 wet</b>	0.017298	0.009511
<b>2010 pre dry</b>	0.014461	0.016415
<b>2011 dry</b>	0.021364	0.024962
<b>Model</b>	0.014949	0.016450

### **A3.2: Details on the CART models of *M. frontalis***

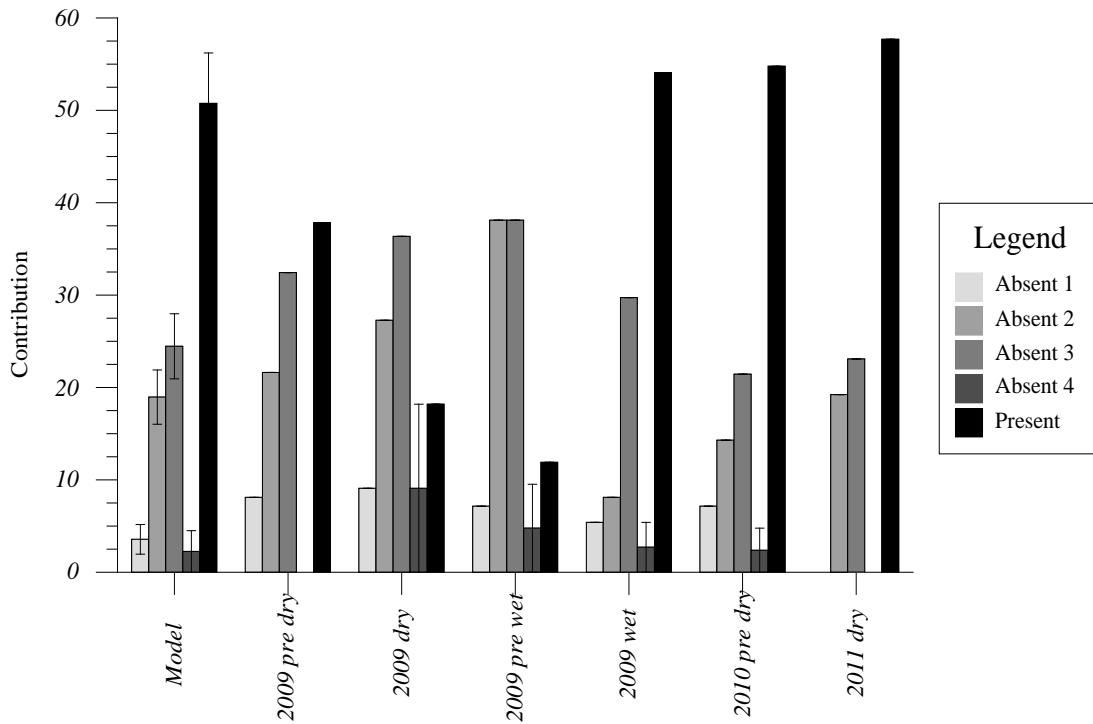
CARTs for presence/absence of *M. frontalis* selected a five or seven leaf model depending on the test trip. The five leaf tree was further analyzed as it was the most robust model that consistently explained a large proportion of the data irrespective of trip (Fig. A3.2). Good predictions were made for the 2009 wet, 2010 pre dry and 2011 dry test trips, but the model was weak in 2009 pre dry, dry and pre wet test trips (Fig. A3.3). Furthermore, although low percentages of false positives (mean: 9.6 %  $\pm$  2.4%SE, range: 4.7% to 18.5%) were recorded for observations in sites where *M. frontalis* was predicted to occur versus all other sites, the sensitivity of these predictions was poor (mean: 39.1%  $\pm$  8.2%SE, range: 11.9% to 57.7%). Because of these poor predictions, the CART model was reduced to two leafs (which was the next model to come out of CART analysis after the seven and five leaf trees).



*M. frontalis*



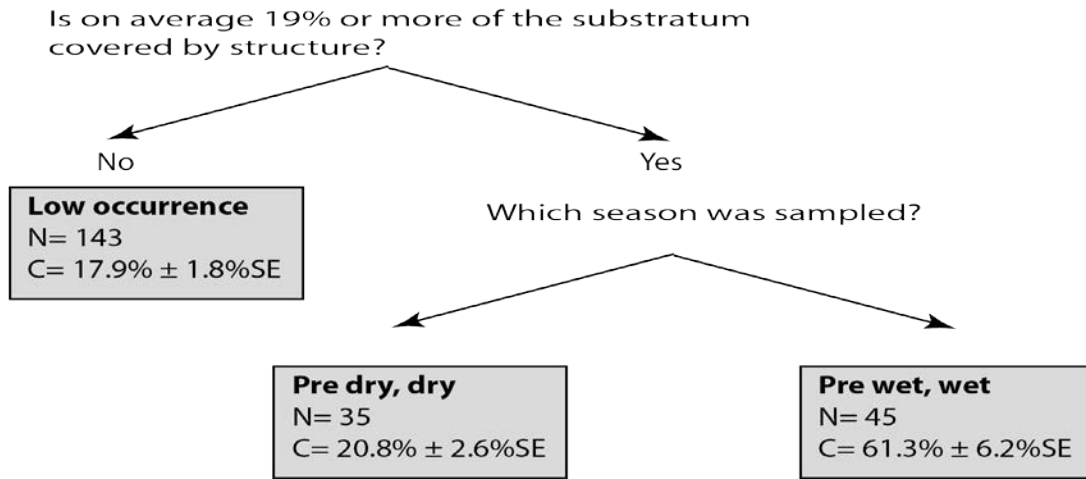
**Figure A3.2** CART model of presence/absence of *M. frontalis* with indication of number of sites (N) and contribution (C) of the presence of *M. frontalis* in each group relative to the total number of presences across all groups per trip, as observed in the training data



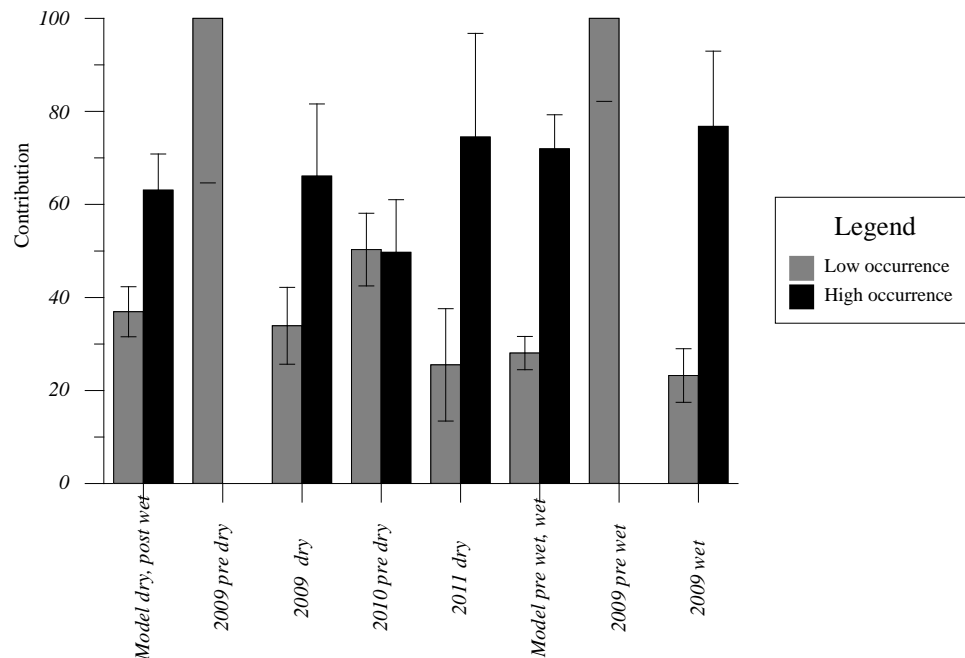
**Figure A3.3** Percentage contribution of the presence of *M. frontalis* in each group relative to the total number of presences across all groups per trip ( $\pm$ SE) for the training and test trips

A CART model was developed in an attempt to further analyze sites where *M. frontalis* was predicted to occur, however this model failed to deliver accurate predictions. Highest relative occurrences were predicted in sites characterized by high root cover, particular in the pre wet and wet season (Fig. A3.4). Overall misclassification was low for the training data (0.000811) and test trips (mean:  $0.000489 \pm 4.47 \cdot 10^{-5}$ , range: 0.000376 to 0.0008535). However, the order and relative contribution of the relative occurrence in each cluster relative to the total relative occurrence across all clusters per trip could not reliably be predicted in half of the test trips (Fig. A3.5). CART analysis did not produce any tree with a lower complexity than the three leaf tree. Hence, no further model could be developed for within-site occurrence of *M. frontalis*.

***M. frontalis***



**Figure A3.4** CART model for relative occurrence of *M. frontalis*, including the number of sites (N) and mean contribution of relative occurrence (C) per cluster relative to the total relative occurrence across all clusters, as observed in the training data

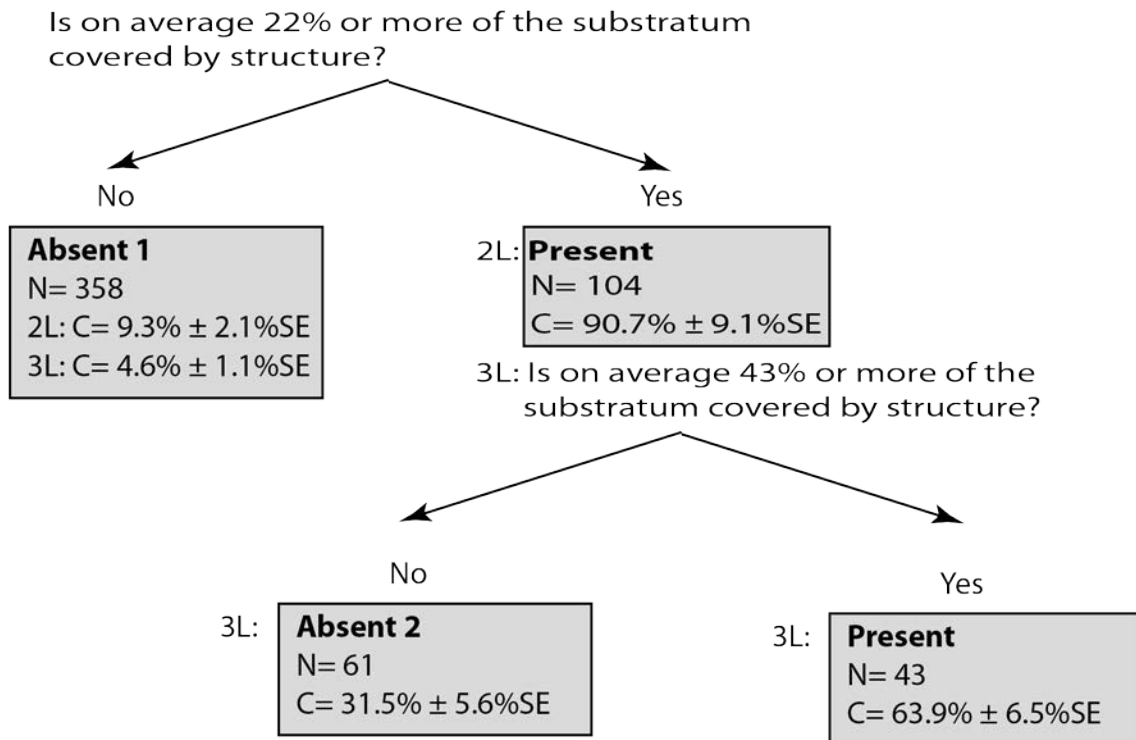


**Figure A3.5** Percentage contribution of the relative occurrence of *M. frontalis* in each cluster relative to the total relative occurrence across all clusters per trip ( $\pm$ SE) in the training data and test trips

### A3.3: Details on the CART models of *M. latifrons*

A three leaf CART model was developed for presence/absence of *M. latifrons* (Fig. A3.6). Despite low percentages of false positives (mean: 3.7% ± 0.4%SE, range: 2.9% to 4.5%), sensitivity of the model predictions were low (mean 28.5% ± 11.4%SE, range: 0% to 62.5%). Consequently the model was reduced to two leafs (which was the next level model proposed by CART analysis).

#### *M. latifrons*



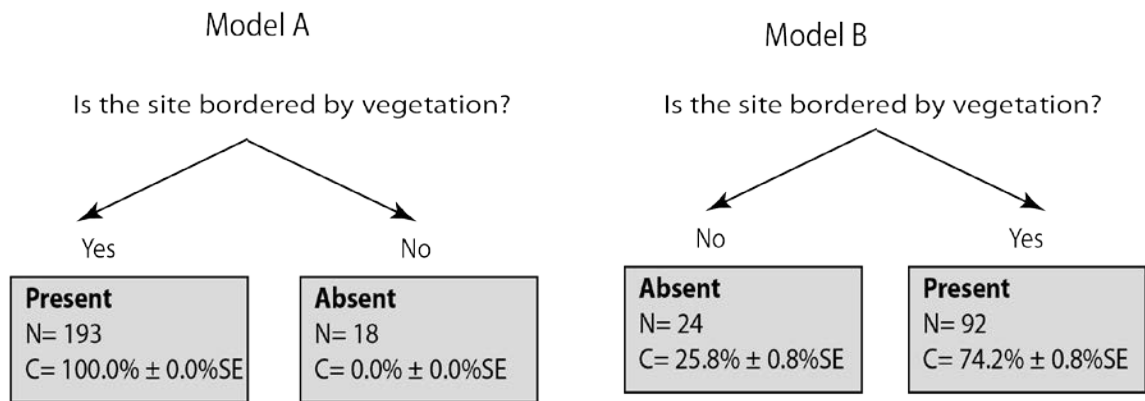
**Figure A3.6** CART model for presence/absence of *M. latifrons*, including the number of sites (N) and the contribution (C) of the presence of *M. latifrons* in each group relative to the total number of presences across all groups per trip, as observed in the training data. 2L indicates results for the two leaf model, 3L, indicates results for the three leaf model

## **Appendix 4: Additional details of the CART models of habitat-association of intertidal crabs in the landscape level ecological model (Chapter 6)**

### **A4.1: Details on the CART model of *U. coarctata***

No single valid CART model was produced using data from all the model systems combined. However, when including system as a categorical predictor, CART analysis revealed two distinct models, one based on training data from the Bohle River, Dougboy Creek and Stuart Creek, the other based on training data from Ross River and Houghton River (Fig. A4.1 model A and B respectively). Model A gives a broad predicted spatial distribution to *U. coarctata*, including 84.7% of sites in the model systems. However, its high percentage of false positive observations in half of the test estuaries (Table A4.1) indicates that many sites where *U. coarctata* was predicted to occur were observed as empty. By contrast, model B predicts a spatially restricted distribution for *U. coarctata*, including only one fourth (24.8%) as many model system sites as model A. However, in nine out of ten test systems model B fails to accurately predict observations of sites that *U. coarctata* occurred in (Table A4.1). Given this very restricted predicted distribution in model B, model A was despite its high percentages of false positives considered a more appropriate model because it leaves the possibility for further development at a later stage.

*U. coarctata*



**Figure A4.1** CART models for predicted presence of *U. coarctata* with indication of number of sites (N) and the observed contribution, expressed in percentage, of occupied sites in each group relative to the total number of occupied sites in the model systems

**Table A4.1** Percentage sensitivity and false positives observed in the model and test systems for the two models of *U. coarctata*

System	Model A		Model B	
	Sensitivity	False positives	Sensitivity	False positives
Bohle River	100.0	48.6	21.4	0.0
Doughboy Creek	100.0	100.0	24.3	40.0
Houghton River	100.0	88.4	73.3	14.0
Ross River	100.0	46.0	75.0	2.0
Stuart Creek	100.0	100.0	61.9	8.3
<b>Model</b>				
average	100.0	76.6	51.2	12.9
St Err	0.0	12.2	11.8	7.2
Baratta downstream	97.1	25.9	14.3	3.7
Baratta upstream	100.0	100.0	37.5	54.5
Bohle River downstream	100.0	29.4	22.6	11.8
Bohle West upstream arm	100.0	33.3	19.0	0.0
Bohle East upstream arm	100.0	100.0	17.9	71.4
Dungeness Creek	100.0	100.0	18.8	4.8
Morris downstream	90.6	73.3	37.5	0.0
Morris upstream	93.9	80.0	32.7	0.0
No Name 2 Creek	100.0	55.2	9.1	0.0
Ross Creek	92.3	51.9	92.3	40.7

#### **A4.2: Details on the CART model of *U. seismella***

No *U. seismella* were sampled in Bohle River. Additionally, very few *U. seismella* were observed in Ross River. Consequently, these systems do not contain much data that could be used to identify habitat associations of *U. seismella*. Hence, the model was built on the remaining three model systems (Fig. 6.3 in the main text).

### **A4.3: Details on the CART model of *M. frontalis***

The sensitivity for observations for the two leaf model of *M. frontalis* presence as developed by CART (Fig. 6.3 in the main text) was low in the model systems of Stuart Creek and Ross River as well as in the test systems: Bohle east upstream arm, Baratta downstream and Ross Creek (Table A4.2). *M. frontalis* have previously been associated with rocky habitats (Shaw and Tibbetts, 2004) and have been observed on rock-walls throughout this study. In this study rock-walls were classified as a type of substratum, without reference to their structural complexity. Nonetheless, rock-walls are often built up from individual boulders which create a high structure habitat. Therefore, an amended model was tested, including rock-walls in the predicted occurrence habitat. The sensitivity for the amended model compared to the original increased in the three systems with rock-walls (Ross River, Baratta downstream, and Ross Creek), while the percentage of false positives remained low. Additionally, the amendment did not influence the sensitivity or percentage of false positives in the other estuaries. Hence, the amended model was used.



**Table A4.2** Percentage sensitivity and false positives in the model and test estuaries for the two models of occurrence of *M. frontalis*

System	Model		Amended model	
	Sensitivity	False positives	Sensitivity	False positives
<b>Bohle River</b>	59.1	15.2	59.1	15.2
<b>Doughboy Creek</b>	88.6	22.2	88.6	22.2
<b>Houghton River</b>	100.0	13.2	100.0	13.2
<b>Ross River</b>	15.4	0.0	61.5	8.9
<b>Stuart Creek</b>	36.4	7.0	36.4	7.0
<b>Model</b>				
<b>Average</b>	59.9	11.5	69.1	13.3
<b>St Err</b>	15.8	3.8	11.3	2.7
<b>Baratta downstream</b>	37.5	0.0	53.1	0.0
<b>Baratta upstream</b>	62.5	4.1	62.5	4.1
<b>Bohle downstream</b>	52.6	12.5	52.6	12.5
<b>Bohle west upstream arm</b>	50.0	32.0	50.0	32.0
<b>Bohle east upstream arm</b>	28.6	0.0	28.6	0.0
<b>Dungeness Creek</b>	81.8	52.4	81.8	52.4
<b>Morris downstream</b>	60.7	5.3	60.7	5.3
<b>Morris upstream</b>	54.8	8.7	54.8	8.7
<b>No Name 2 Creek</b>	93.3	36.1	93.3	36.1
<b>Ross Creek</b>	0.0	0.0	90.5	21.1